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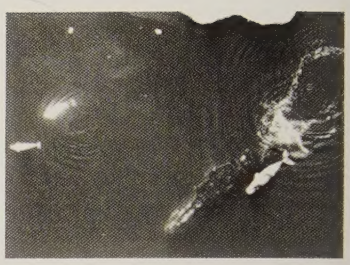

On the cover:
Bowhead whale and calf
with a pair of beluga whales.
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Late Summer Distribution of Cetaceans near Barrow, Alaska: Results from Aerial Surveys Conducted During the Bowhead Whale Feeding Ecology Study, 2007–11

KIM E. W. SHELDEN, JULIE A. MOCKLIN, KIMBERLY T. GOETZ, DAVID J. RUGH, LINDA VATE BRATTSTRÖM, and NANCY A. FRIDAY

ABSTRACT—The aerial survey component of the Bowhead Whale Feeding Ecology Study (BOWFEST) was designed to document patterns and variability in the timing and distribution of bowhead whales, Balaena mysticetus, *and to provide an estimate of temporal and spatial habitat use near Barrow, Alaska. Aerial surveys were conducted from late August to mid-September during the period 2007–11 for a total of 171.1 hours flown. In addition to the focal species, observed species included gray whales,* Eschrichtius robustus; *one humpback whale,* Megaptera novaeangliae; *beluga whales,* Delphinapterus leucas; *ringed seals,* Phoca hispida; *bearded seals,* Erignathus barbatus; *walrus,* Odobenus rosmarus; *and polar bears,* Ursus maritimus. *Small pinnipeds, such as ringed seal and spotted seals,* Phoca largha, *were often difficult to differentiate and identify to species given the relatively high survey altitude of 310 m (1,000 ft).*

Habitat partitioning was evident among the cetacean species observed in greatest numbers: bowhead, gray, and beluga whales. Abundance estimates during this time period ranged from 22 (CV 0.80) to 213 (CV 0.30) bowhead whales, 1 (CV 1.01) to 18 (CV 0.28) gray whales, and 0 to 948 (CV 0.66) beluga whales. Standard deviation ellipses showed each species occupied a unique region within the study area with slight overlaps occurring in some years. Bowhead distribution was oriented along the barrier islands and 20 m isobath on the continental shelf and also included parts of the Barrow Canyon and shelf break that were close to shore. Gray whale distribution oriented along the Barrow Canyon shelf break near the 50 m isobath; while beluga distribution ellipses centered over Barrow Canyon and offshore slope waters. A four-parameter presence-absence model (bathymetry, bathymetric slope, distance from shore, and distance from the shelf break) found both distance from shore and shelf break were significant in predicting the presence of bowhead whales. All four parameters were significant in predicting gray whale presence. Only bathymetry was significant in predicting beluga whale presence.

During the 5-year study, 664 unique bowhead whales were identified from 1,415 photographic images. Observers noted feeding behavior during 7–50% of sightings and 15–49% of photographed whales exhibited feeding behavior in any given year. Of the individual whales that were visually or photographically identified as feeding, 81–90% were in shelf waters, and the majority of those were clustered around the 20 m isobath. More feeding behavior was observed and photographed during years when most sightings occurred on the shelf (2007, 2009, and 2010) but not necessarily in years when bowheads were most abundant in the study area (e.g., 2008 and 2010). The lowest percent feeding both visually and photographically occurred in 2008, the only year whale swim direction was predominately westerly, and open mouth (skim) feeding behavior was not observed.

Although the paucity of individual resightings (based on photographic recaptures) between survey days (3 matches out of 664 identified whales) suggested very low residence times, the photogrammetric sample (654 whales) was largely comprised of juveniles (65%). Young whales typically are unmarked and, therefore, not matched (only 3–6% were highly or moderately marked in at least one zone on the body). All intrayear matched whales moved east of their original sighting location, which was not expected so close to the westbound fall migration.

The BOWFEST aerial study provides a 5-year record of late summer presence of cetaceans in the western Beaufort Sea, adding to the growing body of knowledge on these species and their habitat preferences in this region. This information is particularly important since the western Beaufort Sea is undergoing rapid change as the bowhead whale population continues to grow, other species extend their ranges and increase their numbers in the area, and industrial activity, commercial fishing, and shipping operations are expected to increase in the Arctic as sea ice decreases.

Introduction

Bowhead whales, *Balaena mysticetus,* are distributed in seasonally ice covered waters of the Arctic and subarctic. For management purposes, four bowhead whale stocks are currently recognized by the International Whaling Commission (IWC) (IWC, 2010) and are protected under the U.S. Marine Mammal Protection Act and U.S. Endangered Species Act (Muto et al., 2016). These stocks occur in the Okhotsk Sea (Russian waters), Davis Strait and Hudson Bay (western Greenland and eastern Canadian waters), the eastern North Atlantic (the Spitsbergen stock near Svalbard), and the Bering/Chukchi/Beaufort seas.

The latter is the Western Arctic stock, the largest remnant population and only stock found within U.S. waters (Rugh et al., 2003), generally north of lat. 54°N and south of lat. 75°N in the western Arctic Basin (Moore and Reeves, 1993). This

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stock migrates annually from the Bering Sea through the Chukchi to the Beaufort Sea in the spring. During the spring migration, bowhead whales typically begin arriving in the Barrow (now Utqiaġvik), Alaska, area in early April and continue migrating through until late June (Moore and Reeves, 1993). The fall migration generally begins in early September and continues to mid-October as bowhead whales migrate west across inner shelf waters (Moore et al., 2000) out of the Beaufort and into the Chukchi Sea, as evidenced during previous aerial surveys (Moore et al., 1989; Moore and Clarke, 1992; Richardson[1]; Ljungblad et al.[2]) and satellite-tracking (Quakenbush et al., 2010; Citta et al., 2015).

These whales are important to Native subsistence hunters of Alaska, Russia, and Canada, and hunting is regulated through IWC quotas shared between Alaska and the Russian Federation.[3] Barrow is the largest of the Native subsistence whaling villages, landing roughly half of the total number of bowhead whales hunted each year (Suydam and George[4]).

Bowhead whale feeding activity has been well documented in the eastern Beaufort Sea (e.g., Richardson[1]) but only occasionally observed in other areas along the migratory route, particularly during the fall (Ljungblad et al., 1986; Landino et al., 1994). During the spring, most of the migration appears to be a steady flow of whales traveling from the Chukchi Sea to the Beaufort Sea; however, Carroll et al. (1987) reported what appeared to be feeding behavior (i.e., frequent turns) by some whales. Bowhead whales with mud on their dorsal surfaces were also seen during the spring migration near Barrow, indicating that they were near the sea bottom, presumably feeding on epibenthic prey (Mocklin et al., 2012).

Braham et al. (1979) stated that Eskimo whalers had occasionally seen bowhead whales near Point Barrow during the summer, some of which were feeding east of Point Barrow close to shore. In 1989, bowhead whale feeding activity was reported off Barrow from late July to mid-August (George and Carroll[5]). Moore (1992) compiled additional records of bowhead whales in the northeastern Chukchi Sea, comprising 26 sightings that occurred from late July to early September between 1975 and 1991. These sightings indicated that bowhead whales may occupy areas near Barrow during the summer months.

In the early 2000's, local hunters reported bowhead whales feeding in echelon formation (i.e., animals lined up in a v-shaped pattern, head to tail) near Barrow in late August (George et al.[6]). Whales with muddy heads and open mouths and lunge feeding were also observed in early September in 2005 and 2006 (Moore et al., 2010a, b). These observations suggested a need for a more systematic, scientific approach to assess the relative scale of feeding and the consistency of this behavior relative to season, year, age-class, etc., together with relevant ecological parameters, such as bathymetry, currents, temperatures, ice conditions, and prey availability.

The Bowhead Whale Feeding Ecology Study (BOWFEST) was initiated in May 2007 through an interagency agreement (formal title: "The bowhead whale feeding variability in the western Beaufort Sea: feeding observations and oceanographic measurements and analyses") between the U.S. Department of the Interior's Minerals Management Service (MMS, now the Bureau of Ocean Energy Management, BOEM) and the Alaska Fisheries Science Center's National Marine Mammal Laboratory (NMML, now Marine Mammal Laboratory, MML). The goal of this 5-year study was to facilitate future oil and gas development-related mitigation by estimating relationships among bowhead whale prey, oceanographic conditions, and bowhead whale feeding behavior in the western Beaufort Sea, with emphasis on identifying predictable aspects in those relationships. The study focused on late summer oceanography and prey densities relative to bowhead whale distribution over continental shelf waters between the coast and lat. 72°N, and between long. 152°W and 157°W, which is north and east of Point Barrow, Alaska. Projects were timed to end at least one week before the bowhead whale subsistence hunt commenced.

The BOWFEST study included several components. Aerial surveys and passive acoustic monitoring provided information on the spatial and temporal distribution of bowhead whales in the study area. Oceanographic sampling identified sources of zooplankton prey available to whales on the continental shelf and the association of this prey with physical (hydrography, currents) characteristics which may affect mechanisms of plankton aggregation. Prey distribution was characterized by examining temporal and spatial scales of the hydrographic and velocity fields in the study area, particularly relative to oceanic frontal features.

Reports compiling aerial survey data and other components of BOW-

[1]Richardson, W. J. (Editor). 1987. Importance of the eastern Alaskan Beaufort Sea to feeding bowhead whales, 1985-86. Rep. to U.S. Minerals Manag. Serv. by LGL Inc., NTIS No. PB88-150271, 547 p.

[2]Ljungblad, D. K., S. E. Moore, J. T. Clarke, and J. C. Bennett. 1987. Distribution, abundance, behavior and bioacoustics of endangered whales in the Alaskan Beaufort and Eastern Chukchi Seas, 1979-86. OCS Study MMS 87-0039, NOSC Tech. Rep. 1177 to U.S. Minerals Manag. Serv., Anchorage, Alaska, NTIS PB-88-116470, 391 p.

[3]Canada withdrew from the IWC after enactment of the moratorium on commercial whaling in 1982. Currently, the Department of Fisheries and Oceans (DFO) manages Native subsistence requests to hunt bowheads by issuing licenses (http://www.sararegistry.gc.ca/default.asp?lang=En&n=D67BEABF-1, accessed 6 Apr. 2015)

[4]Suydam, R. S., and J. C. George. 2012. Subsistence harvest of bowhead whales (*Balaena mysticetus*) by Alaskan Eskimos, 1974 to 2011. Pap. SC/64/AWMP8 pres. to IWC Sci. Committ., May 2012, 13 p.

[5]George, J. C., and G. M. Carroll. 1989. August sightings of bowhead whales in the Point Barrow to Cape Simpson region. Unpubl. ms., Memorandum to Benjamin P. Nageak dated 21 August 1989. Avail. at North Slope Borough, Dep. Wildl. Manag., P.O. Box 69, Barrow, Alaska, 99723.

[6]George, J. C., S. Moore, W. Koski, and R. Suydam. 2006. Opportunistic photo identification survey: Barrow autumn 2005. Abstr. pres. at Workshop II: Bowhead whale stock structure studies in the Bering, Chukchi, and Beaufort Seas (BCBS) 21-22 March 2006, Seattle, Wash.

FEST (passive acoustics, oceanography, tagging, small boat surveys, and stomach analyses) were published annually to the MML website[7] for each year (2007–11). Results of this research may help explain the increased occurrence of bowhead whales feeding in the western Beaufort Sea (U.S. waters), west of the typical summer feeding aggregations in the Canadian Beaufort Sea. Increased understanding of bowhead whale behavior and distribution is needed to minimize potential impacts from human development in the Arctic. Information from this study will be used by BOEM for pre- and post-lease analysis and documentation under the National Environmental Policy Act (NEPA) for Beaufort and Chukchi Sea Lease Sales.

Here we present results from the 5 years of aerial survey data acquired during late summer, 2007–11. The BOWFEST aerial survey included a combination of systematic transects and photography to document patterns and variability in the occurrence of individual bowhead whales as well as provide descriptions of spatial habitat use within the sample period. Aerial project data were examined to determine whether bowhead whales were traveling through the area or were effectively residents during late summer. Time spent feeding near Barrow in late summer, as well as the consistency of this behavior relative to location within the study area, year, and age class (using whale size as a proxy for age) were also documented.

Methods

Study Area

The study area included continental shelf waters and deep submarine canyons between long. 157° W and 152° W and from the Alaska coastline (barrier islands) to lat. 72° N (Fig. 1). This area was divided into a two-part sampling scheme that included tracklines within an inner box (7,276 km^2) and an outer box (12,152 km^2).

[7]Annual reports from the BOWFEST and BWASP projects are available at: http://www.afsc.noaa.gov/nmml/cetacean/bwasp/bowfest.php

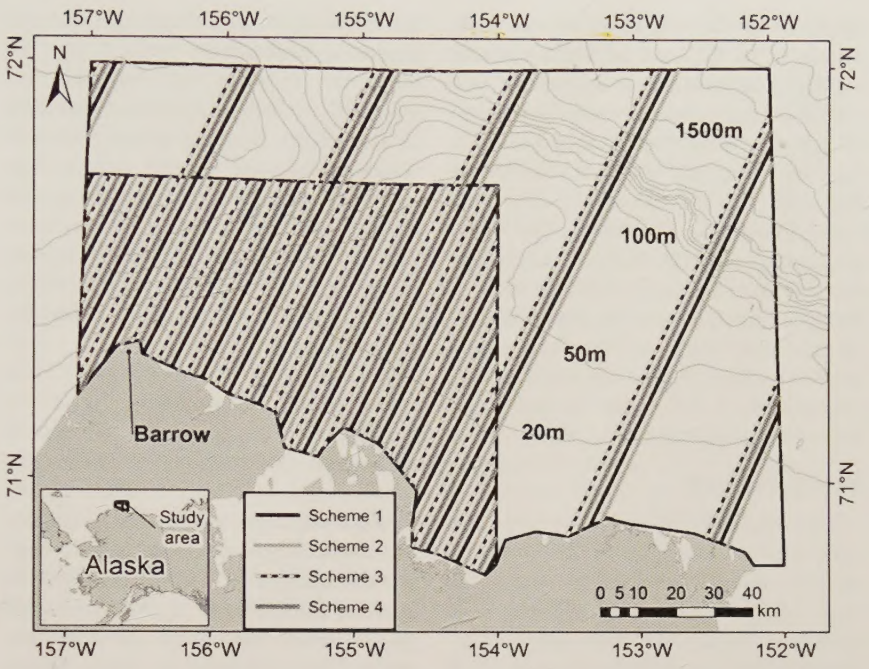

Figure 1.—The four survey schemes for the 2009–11 BOWFEST aerial surveys. Survey schemes differed slightly for 2007 and 2008 (text footnote 7). Most of the effort was concentrated between long. 157° W and 154° W and between the coastline and lat. 71° 44'N (the inner box boundaries).

Sampling Scheme

The design of the sampling scheme was based on 6 years of data (2000–05) from the Bowhead Whale Aerial Survey Project (BWASP[7]) conducted by MMS. These data provided information on bowhead whale relative density (whales per km surveyed) northeast of Barrow. This helped stratify and ultimately determined the distribution and quantity of survey effort relegated to the inner and outer boxes of the BOWFEST study area. From the BWASP data, the relative density of bowhead whales in the inner box was approximately six times greater than in the outer box. Using equations 7.1, 7.2, and 7.4 from Buckland et al. (1993), the total effort needed in each of the two boxes was calculated to obtain a detection probability sufficient for determining relative densities of whales.

Trackline orientation was based on predetermined oceanographic tracklines which were oriented in a northeasterly direction at 66° True (i.e., perpendicular to the generalized coastline). The study area contained approximately 5,011 km of trackline, of which 3,554 km were in the inner box and 1,457 km in the outer box (Fig. 1). Tracklines were flown sequentially west to east in order to minimize the probability of resighting the same whale(s) should the westward migration be underway.

The tracklines in the inner box were spaced 2 km apart while lines in the outer box were 8 km apart. The placement of the first (most westward) survey line in the inner box (closer to Barrow) was determined by random selection. The same random value to calculate placement of the first line in both boxes was purposely used to align the tracklines in the inner and outer boxes of the study area (Fig. 1). This method simplified flight logistics and minimized transit time between tracklines. Subsequent tracklines were parallel to the first trackline.

Sampling schemes were devised

by shifting the trackline array short distances to the east or west, removing the likelihood that any tracklines would be flown twice within a season. The first scheme (Scheme 1) was created by selecting the first line from the west side of the study area and every fourth line thereafter. The three remaining schemes were created using the same method, with the second through fourth lines from the west side of the study area. As a result, tracklines for each scheme were spaced approximately 8 km apart in the inner box of the study area (Fig. 1).

Survey Protocol

The BOWFEST aerial survey aircraft was a NOAA Twin Otter.[8] These aircraft have twin turbine engines, high wings, and approximately 5 h of flying endurance. Two large bubble windows provided views ahead of and beneath the plane for the left- and right-side observers. An open belly window/camera port allowed for vertical photography. Communication among observers, pilots, and the data recorder occurred via an intercom system. Aircraft speed was approximately 185 km/h (100 knots). Survey altitude was 310 m (1,000 ft); most photography passes were between 210 m (700 ft) and 240 m (800 ft).

During flight, effort was categorized as deadhead (transiting between tracklines or locations), trackline (systematic search along designated transects), circling (breaking from the trackline mode to investigate a sighting), or photo mode (circling with the specific intent to collect photographs of whales).

The data recorder used a custom-built aerial survey software program installed on a laptop computer which interfaced with a portable global positioning system (GPS–Garmin 76 CSx). The program saved sighting information, weather parameters, effort (on or off), crew position, and photo data into an Access database. Position information (latitude, longitude, speed, altitude, and heading) was recorded automatically every 5 sec via the GPS; all other data were entered manually including each start and stop of a trackline. Specific data entries for weather included overall percent ice cover, ice type (categorized using the Observers Guide to Sea Ice[9]), sky condition, and sea state (Beaufort scale). Glare, visibility angle, and visibility quality were recorded individually for each side of the aircraft.

To obtain the visibility angle, observers used an inclinometer (0° = horizontal; 90° = straight down) to accurately determine the searchable distance out each side of the aircraft. Visibility quality within the given inclinometer angle was one of five subjective categories from excellent to useless; for example, a record of "20° good" meant that from the trackline out to 20° (0.8 km), sighting conditions were good, and farther from the trackline (<20°) the visibility worsened and was not recorded. Unsurveyed areas (i.e., off effort) included portions of the trackline where both observers rated visibility quality as poor or useless. All marine mammal sightings included date, time, observer, inclinometer angle, group size, reaction to plane, and species. For bowhead whale sightings, observers also reported calf number, travel direction, sighting cue, dominant behavior, and group composition. Any vessels within the study area were also noted.

Immediately upon sighting a marine mammal, the observer reported group size and species to the data recorder. If the sightings occurred ahead of the aircraft an inclinometer angle and any observable reaction to the aircraft were recorded as the aircraft came abeam of the sighting. When a whale appeared to be swimming at a steady speed (i.e., not feeding, resting, or displaying any other type of cetacean behavior), it was recorded as "traveling," and a swim direction was given relative to an analog clock (aircraft nose is 12 o'clock) and later converted relative to global directions (0°T = north). The aircraft deviated from the trackline only when an observer was unable to identify the species of a large cetacean. If bowhead whale sightings occurred while on transect, the trackline was typically completed before going off effort to begin photographic passes. This method allowed for a systematic search effort along tracklines and minimized confusion in reporting sightings while off effort.

Photographic Protocol

Objectives of the photographic portion of the BOWFEST aerial survey included

1) Examining bowhead images for within year (intrayear) matches and across study year (interyear) matches to determine residency times and site fidelity, respectively;
2) Measuring bowhead lengths to determine age class distribution within the study area; and
3) Noting evidence of bowhead feeding behavior (such as mud on body, open mouth, and fecal plumes).

Photographs were taken through a port in the belly of the aircraft located aft of the landing gear. The port was covered in optical quality glass in 2007; however, glare on the window was problematic, so the glass was removed for the 2008–11 surveys. The photographic system evolved over the course of the BOWFEST study. At minimum, two cameras were used with one dedicated to obtaining images for the age class study (photogrammetry) and the other to document residence times and feeding behavior (photo-identification). Date and time on all cameras were synchronized with the date and time on the GPS unit at the beginning of each survey. To obtain usable images for photogrammetry, it was important to keep this camera level and the lens fixed and focused to near infinity and taped to impede rotation.

In 2007, when both cameras were handheld, the photographer using the small, fixed lens (55 or 85 mm) strove to hold the camera as level as possi-

[8]Mention of trade names or commercial firms does not imply endorsement by the National Marine Fisheries Service, NOAA.

[9]http://archive.orr.noaa.gov/book_shelf/695_seaice.pdf

ble (no angling) to obtain usable images for photogrammetry. In 2008 and 2009, the photogrammetry camera was housed in a forward motion compensation (FMC[10]) mount (installed on the port side of the belly window) which used a rocker mechanism to counter the forward velocity of the relative ground speed. In 2010 and 2011, three cameras were installed side by side in an FMC mount. The center camera was prioritized for photogrammetry and the left and right cameras were set to overlap the center camera by 20% by angling them slightly inward. These cameras were integrated with an autonomous radar altimeter (Honeywell AA300 model) in order to collect precise altitudes each time the cameras were fired. Unlike the handheld cameras, mounted cameras were fired using a custom built data acquisition system that automated the retrieval of data (i.e., altitude, time of camera firing, frame number, aircraft speed, and focal length of the camera lens). A keystroke on the computer triggered cameras to continuously fire so that each consecutive image overlapped the previous photo by 60%, adjusted for altitude.

Cameras recorded in RAW format, 21.0 megapixels (5616 x 3744) images and were set to shutter priority (1/1000 sec) and ISO 400–800. After breaking trackline effort, passes were flown over each bowhead group until the observers were confident that most whales in the area had been photographed. During each photographic pass, the forward observer provided a countdown to alert the photographer(s) and data recorder when a whale was about to appear under the aircraft.

Each year, calibration targets were photographed using the same cameras and lenses used to photograph bowhead whales. A land target was used in all years, and in 2008 and 2009, a floating water target was added to look for possible discrepancies between radar altimeter performance over land and water (Mocklin et al., 2010). Altitudes for photogrammetric passes were at 30.5 m (100 ft) intervals ranging from 152 m (500 ft) to 457 m (1,500 ft), weather permitting. Measurements from the photographs provided a linear regression correction factor for the altimeter readings. This correction factor was then applied to photographs of bowhead whales used in the photogrammetric study.

After each survey, all photographs were geo-referenced using RoboGEO[11], and RAW images were converted to TIFF (2007–09) or JPG (2010–11). Once geo-referenced, all images and associated metadata were sent to LGL, Inc. for analysis of whale lengths (Koski et al., 1992; 2006). Only images assigned grades of 1–6 were used in the photogrammetric analysis (Koski et al., 2006).

Processing for photo-identification of individual whales began with cropping and labeling of images. Whale images were scored for quality and identifiability (Rugh et al., 1998). Quality scores of 1+ (best), 1-, 2+, 2- or 3 (worst) were assigned to four zones on the whale's body: rostrum, mid-back, lower back, and flukes. A zone scored as 3 was considered inadequate for purposes of reidentifying a whale. Identifiability scores for each zone included H+ or H- (highly marked), M+ or M- (moderately marked), U+ or U- (unmarked), or X (meaning the zone was not depicted clearly enough in the photo to determine mark status). Scores of X almost always corresponded to quality 3.

Data Analysis

Distribution maps for all cetacean sightings were created using ArcGIS 10.1 (ESRI, Redlands, CA, USA). Bowhead whale sightings were linked to a raster bathymetry file (name: IBCAO_V3_500m_RR; Jakobsson et al., 2012) to determine depths (in meters) associated with each sighting. Trackline data were analyzed by day and scheme for each survey year. Segments of on-effort trackline with respective length were linked to each cetacean sighting that had an inclinometer angle.

Abundance estimates and sighting rates were computed for the cetacean species most frequently encountered during the study: bowhead whales, gray whales, *Eschrichtius robustus*; and beluga whales, *Delphinapterus leucas*, using distance sampling methods (Buckland et al., 2001, 2004) as implemented in the Mark-Recapture Distance Sampling (mrds) package (Laake et al., 2007) for R (R Development Core Team, 2008). Both conventional (CDS) and multiple covariate distance sampling (MCDS) approaches were used. To increase the sample size when fitting the detection function, sightings from all years were combined with additional-effort sightings from the transit legs.

To improve the fit of the detection functions, the perpendicular distance data for bowhead whales were truncated at 6 km and binned into 0.5 km bins to 3 km and then 1 km bins to 6 km. It was not necessary to truncate the perpendicular distance data for beluga or gray whales. The perpendicular distance data for beluga whales was binned into 0.2 km bins and for gray whales into 0.25 km bins to 1.5 km and 0.75 km thereafter.

Five covariates were explored: sea state, group size (as square root), observer, glare, and sky condition. For gray whales, the four observers with seven or fewer sightings were combined into a single category and the sky variables of light fog, low ceiling, and precipitation were combined into a single category. Hazard-rate and half-normal models were fit without covariates, and with all possible combinations of 1–5 covariates, resulting in 64 candidate models for each species.

The best-fit model for the detection function was selected using Akaike's Information Criteria (AIC) which seeks to maximize the likelihood and minimize the number of model parameters (Burnham and Anderson, 2002). Models with $\Delta AIC \leq 2$ are considered well supported by the data and are presented here for comparison, but densi-

[10]http://www.aerialimagingsolutions.com/fmc-mount.html

[11]http://www.robogeo.com/home/

Table 1.—Survey days, flight hours, and percent time spent on effort on trackline (in parentheses) during BOWFEST aerial surveys, late August to mid-September during the period 2007–11. Black boxes depict survey days; gray boxes depict days the aircraft and crew were available but precluded from flying due to weather (fog (F), low cloud cover (LC <500 ft ceilings), winds (W >20 kts),) rain (R), snow (S)), or mechanical issues (MI).

	Year				
Day	2007	2008	2009	2010	2011
22-Aug	LC				
23-Aug	6.7 (38%)				
24-Aug	3.8 (21%)				
25-Aug	F/LC				
26-Aug	LC/W				2.0 (0%)
27-Aug	no aircraft	LC/W			F
28-Aug	no aircraft	LC/W			F
29-Aug	no aircraft	4.9 (35%)			F
30-Aug	no aircraft	3.9 (25%)	W		F
31-Aug	no aircraft	LC/W	W	no fuel	F
1-Sept	no aircraft	LC/W	W	0.9 (0%)	F
2-Sept	no aircraft	W	5.7 (46%)	no fuel	3.2 (35%)
3-Sept	no aircraft	F/W	W/R	F/LC/R	F
4-Sept	no aircraft	LC	4.3 (36%)	F	F
5-Sept	F/LC	6.3 (39%)	W	F	6.9 (59%)
6-Sept	4.1 (1%)	6.4 (36%)	W/S	5.3 (48%)	W
7-Sept	5.5 (46%)	R/F/LC	4.4 (7%)	F/LC	4.2 (73%)
8-Sept	LC	R/F/LC	F/LC/R/S	3.9 (44%)	4.8 (57%)
9-Sept	2.5 (53%)	R/F/LC	F/LC/R/S	F	4.5 (54%)
10-Sept	LC	R/F/LC	F/LC/R/S	F	W
11-Sept	8.2 (57%)	6.7 (46%)	F/LC/R/S	F	W
12-Sept	LC/F/W	F/LC	F/LC/R/S	9.5 (62%)	8.2 (58%)
13-Sept	aircraft maintenance	10.9 (49%	F/LC/R/S	2.1 (26%)	8.0 (45%)
14-Sept		MI	1.0 (0%)	F/W	4.3 (63%)
15-Sept		2.4 (18%)	2.7 (33%)	4.4 (60%)	W
16-Sept		1.1 (40%)	LC	LC/W	0.7 (39%)
17-Sept		W	LC	5.2 (52%)	
18-Sept				1.6 (0%)	
Total	30.8 (39%)	42.6 (39%)	18.0 (30%)	32.9 (49%)	46.8 (53%)

ty and abundance were computed with the best-fit model. On-effort sightings were separated by strata for estimating group size, sighting rates, density, and abundance. Data were not collected to determine animals missed on the trackline (perception bias) or animals submerged when the plane passed (availability bias). Therefore, corrections were not made for these biases and g(0), the sighting probability on the trackline, was assumed to be 1.

Distributions were also compared among these three cetacean species. Each species distribution each year was weighted by group size using 1SD "directional distribution" ellipses in ArcGIS which captured approximately 68% of the sightings. Additional analyses were conducted on sightings in the inner box then compared to combined inner and outer box sightings for all years to determine if distributions were significantly different.

To describe the presence or absence of sightings as a function of environmental, or explanatory, variables, all bowhead, gray, and beluga whale sightings within the inner box were linked to bathymetric depth (BATHY), bathymetric slope (SLOPE), distance from the shelf break (100 m isobaths - DISTSHELF), and distance from shore (DISTSHORE). The resolution of all spatial data layers in ArcGIS was 100 × 100 m. For each whale species, random locations were generated to match the number of sightings within the inner box.

To examine the structure within the data, a logistic regression model was employed. After examining the variables for colinearity, we used a backward elimination method to assess the significance of the environmental variables in predicting habitat use. AIC was used to select the final model for each of the three species. The diagnostic accuracy of each of these models was determined using a receiver operating characteristic (ROC) curve which is able to detect a signal in the presence of noise. The area under the ROC curve (AUC) ranges from 0 (no discrimination ability) to 1 (perfect discrimination ability against false positives and false negatives). Values greater than or equal to a threshold value (0.40 for beluga, 0.51 for bowhead, and 0.61 for gray whales) were classified as preferred habitat.

Swim direction at the time of each sighting was compared for all bowhead whales with travel noted as the primary behavior. A Rayleigh uniformity test (KCS, 2012), run in the software program Oriana, determined whether clustering around a mean swim direction occurred within each survey year. Feeding behaviors (mud on the whale, mouth open, and fecal plume) were reported by the observers and documented during the photography effort. We examined percentages of feeding behavior reported by observers and captured photographically each year. We also mapped the locations of sightings and photographs documenting these behaviors.

For residency times, all images were compared to determine if individual whales were photographed multiple times over multiple days (multiple images of an individual obtained within a single day were considered to be a single sample). Following intrayear comparisons, whale images were compared across all BOWFEST years to look for evidence of seasonal site fidelity. We also noted if any matched whales appeared to be feeding.

Using photogrammetric lengths, bowhead whales were sorted into specific age classes (calf, juvenile, and adult per Koski et al. (1992, 2006)) to help determine age structure within the study area over the five-year period. Length data were binned and graphed by year and overall. We also present length data for the subset of whales that appeared to be feeding.

Results and Discussion

Survey Effort

Aerial surveys were conducted in the BOWFEST study area from the end of August to mid-September during the period 2007–11 for a total of 171.1 hours flown. Most in-flight, on-effort survey time was spent on trackline (Table 1). A total of 10.3 hours of survey time (6.3% of all flight time)

Table 2.—Survey trackline effort during BOWFEST aerial surveys within the inner and outer boxes of the study area from late August to mid-September during the period 2007–11.

Year	Inner box (km surveyed)	Inner box (% covered)	Outer box (km surveyed)	Outer box (% covered)
2007	2071.2	58%	208.6	4%
2008	2637.3	74%	445.5	9%
2009	1007.0	28%	0.0	0%
2010	2653.0	75%	407.5	8%
2011	4134.4	116%	476.5	10%

was in poor or useless viewing conditions, and there were 57 days without surveys due to weather (56% of all days when the aircraft was available for flying).

On flight days, 56% of the survey effort was over calm seas with few whitecaps (Beaufort Sea States 3 or lower). Sea states of 3 and lower are considered optimal for detecting most marine mammal species; however, observers reported 91% of survey effort as "fair" or better, suggesting despite higher sea states the observers remained confident that bowhead whales could be detected. The greatest percentage of effort was focused within the inner box of the study area (Table 2, Fig. 2).

Sightings

Marine mammals observed within the study area were identified to species whenever possible (Table 3). Over 1,000 sightings of marine mammals were recorded during the 5-year study. In addition to the focal species (bowhead whales) observed species included gray whales, one humpback whale, beluga whales, ringed seals, *Phoca hispida*; bearded seals, *Erignathus barbatus*; walrus, *Odobenus rosmarus*; and polar bears, *Ursus maritimus*. Small pinnipeds, such as ringed seals and spotted seals, *Phoca largha,* were often difficult to differentiate and identify to species given the relatively high survey altitude of 310 m (1,000 ft) (Table 3).

Beluga whales were the only odontocetes observed (Fig. 3). Though not seen during BOWFEST aerial surveys, harbor porpoise, *Phocoena phocoena,* also occur off Barrow (Suydam and George, 1992), and occasionally killer whales, *Orcinus orca* (Braham and Dahlheim, 1982; Clarke et al.[12]). Beluga whales were seen in all years except 2009, and although survey effort was limited that year, sighting numbers were also low the preceding and following year. In general, beluga whales were found in slope waters and over the deeper waters of Barrow Canyon; however, in 2011, groups were also observed swimming near barrier islands (Fig. 3).

Three species of baleen whales were seen during BOWFEST: bowhead, humpback, and gray whales. In 2009, a lone humpback whale associated with a group of gray whales was observed in shelf waters off Point Barrow (Fig. 4). Gray whales were present during every survey year, and sighting numbers were consistent year to year with the exception of 2010 when their numbers were at their lowest and bowhead whales at their highest (Table 3). Almost all gray whale sightings occurred on the 50 m isobath along Barrow Canyon (Fig. 4).

Bowhead whale presence and sighting numbers were variable from year to year (Table 3). There was no apparent increase in bowhead sightings during the survey period as might be expected with the onset of the fall migration (Table 4). Most sightings occurred over continental shelf waters east of Point Barrow (Fig. 5). In 2007, the aerial team found whales in shelf waters (on the 20 m isobath) on 2 days in late August, but none were found in September. In 2008, aerial observations included a few whales scattered in Barrow Canyon, large groups along the canyon shelf break north of Barrow, some groups along the 20 m isobath on the shelf, and small numbers in deeper waters to the east. In 2009, most bowhead whale sightings occurred along the 20 m isobath, with a few whales in Barrow Canyon and along the shelf break near Barrow. In 2010, there was no inshore-offshore bias in bowhead whale distribution. The aerial team found large numbers of whales near the barrier islands, closer to shore than during any other study year, and spread across the shelf to the slope. In 2011, whales were in Barrow Canyon and deeper waters to the east, not on the shelf. Most sightings in 2011 occurred in waters >100 m deep. With sightings binned into four depth ranges (Fig. 6), most bowhead whales were in relatively shallow water; 72% were in water depths < 30 m and 80% in waters < 50 m. The remaining bowhead whales were in waters between 50 and 100 m (8%) and greater than 100 m (12%), the latter largely driven by distribution in 2011.

Abundance

The detection functions for the best-fit models (minimum AIC) for bowhead, gray, and beluga whales are shown in Figure 7. Table 5 includes all well-supported ($\Delta AIC \leq 2$) models compared to the best-fit model for each species. For bowhead whales, the hazard rate model with the square root of group size and observer as covariates was the best-fit model. For gray whales and beluga whales, the half-normal model with the square root of group size as a covariate were the best-fit models. Group size was the most important variable as it was a covariate in all the models with $\Delta AIC \leq 2$ for all three species with the exception of one beluga model that had no covariates (Table 5). For bowhead whales, observer was also an important variable and present in all bowhead models with $\Delta AIC \leq 2$.

Encounter rate, group size, density,

[12]Clarke, J. T., C. L. Christman, A. A. Brower, and M. C. Ferguson. 2013. Distribution and relative abundance of marine mammals in the northeastern Chukchi and western Beaufort seas, 2012. Annu. Rep., OCS Study BOEM 2013-00117, 364 p., Natl. Mar. Mammal Lab., Alaska Fish. Sci. Cent., NMFS, NOAA, 7600 Sand Point Way NE, F/AKC3, Seattle, WA 98115-6349 (http://www.afsc.noaa.gov/nmml/PDF/COMIDA-2012-Report.pdf)

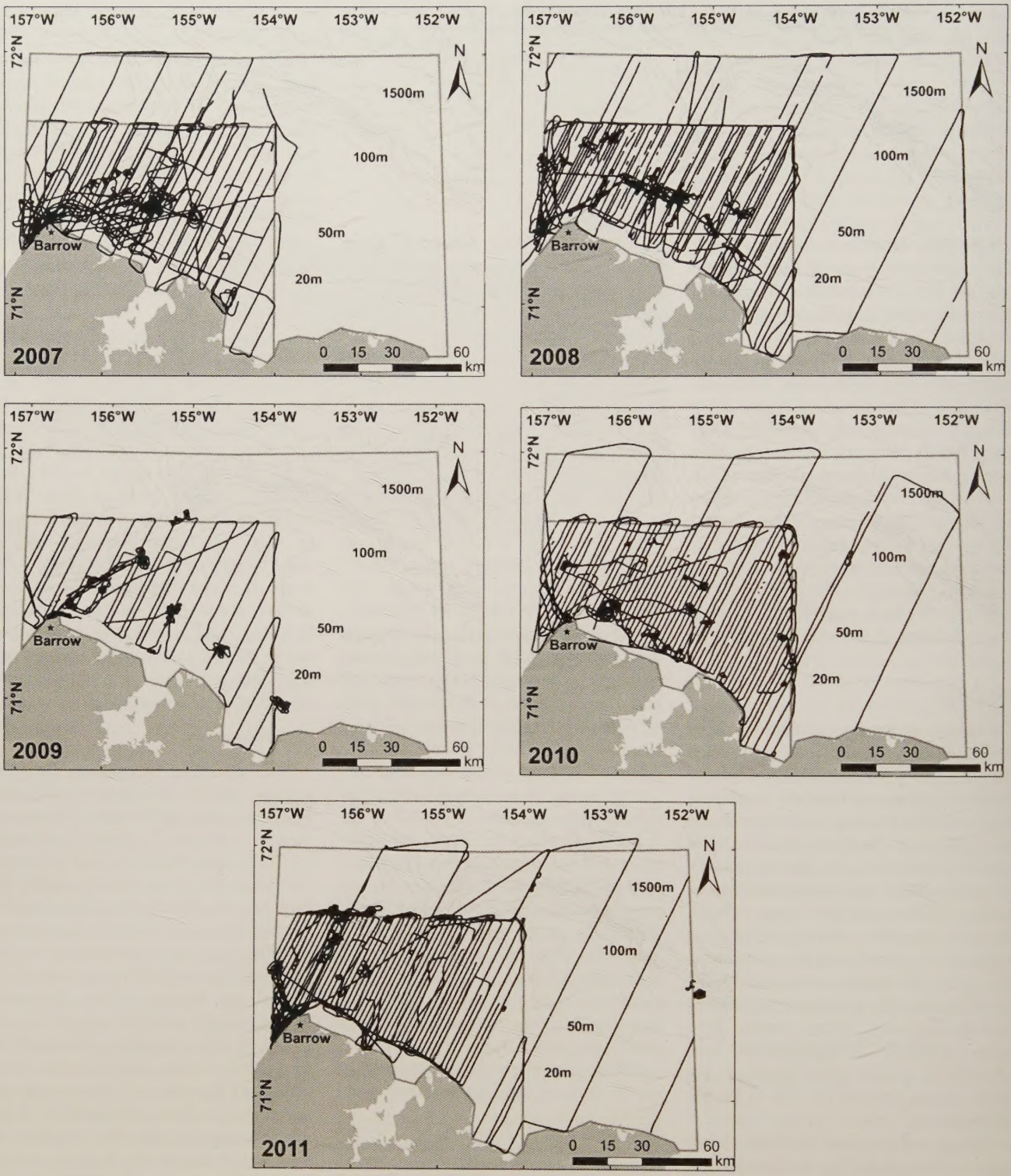

Figure 2.—All search effort, including transect, circling, and photo effort for each BOWFEST aerial survey from late August to mid-September during the period 2007–11.

Table 3.—Summary of marine mammal sightings and counts made during BOWFEST aerial surveys from late August to mid-September during the period 2007–11. Bowhead whale counts usually increased when off trackline to circle or photograph groups of whales (in parenthesis). Bowhead whales observed during transit between transects were also included in the grand total number.

Marine mammal	Sightings/count (count after departing trackline to circle) per year					
	2007	2008	2009	2010	2011	Total
Bowhead whale	16/35(68)	56/191(195)	29/35(55)	102/396(452)	18/10(68)	221/667(838)
Gray whale	20/29	22/39	22/30	6/10	26/34	96/142
Beluga whale	18/30	2/2		2/5	95/460	117/497
Humpback whale			1/1			1/1
Ringed seal	73/119	4/6	2/2	8/40		87/167
Bearded seal	31/89	9/9	6/6	3/3	21/22	70/129
Walrus	65/255		3/12	1/2		69/269
Polar bear	2/2	4/5		16/23	6/6	28/36
Unid large cetacean		13/13	6/7	1/1	6/9	26/30
Unid small cetacean					1/1	1/1
Unid pinniped	10/12	86/139	25/52	61/86	117/237	299/526
Total	235/571	196/404	94/145(162)	200/566(553)	290/779(836)	1,015/2,465(838)
Sightings/km	0.103	0.064	0.093	0.065	0.063	

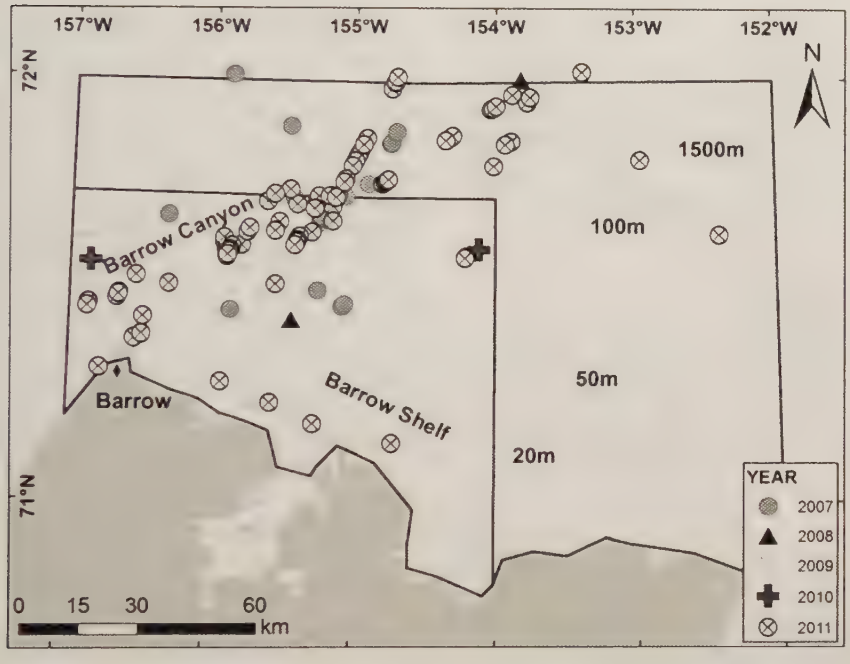

Figure 3.—Locations of beluga whale sightings during BOWFEST aerial surveys from late August to mid-September during the period 2007–11. Note: there were no sightings in 2009.

and abundance were estimated using the best-fit detection function model and are presented in Tables 6 and 7 for each species by year and survey domain. Estimated encounter rates (#/km) (Table 6) and density (#/km^2) (Table 7) for bowhead whales were generally higher in the inner box of the study area in all years. With the exception of 2007, estimated group sizes were < 3 whales (Table 6). Estimated abundance for the inner box was also higher than in the outer box although the differences were not statistically significant (Table 7). Gray whales were only encountered in the inner box. Estimated group sizes were < 2 whales in all years but 2008 (Table 6). Abundance estimates and densities were the lowest in 2010 (Table 7), following a decline in encounter rates and density from 2007 to 2009. Gray whale numbers rebounded to 2007 levels in 2011. When belugas were present in the outer box of the study area (2007 and 2011), encounter rates were 2.6–8.2 times lower in the inner box (Table 6). Estimated abundance in 2007 and 2011, respectively, ranged from 21 (CV = 0.76) to 280 (CV = 0.90) (inner vs. outer box) and 123 (CV = 0.43) to 825 (CV = 0.75) (inner vs. outer box). When not present in the outer box, belugas were rarely encountered in the inner box of the study area (0.0004/km, CV = 1).

Habitat Preferences

Habitat partitioning between bowhead and gray whales was evident in all survey years, and among bowhead, gray, and beluga whales in those years when belugas were observed in large numbers (Fig. 8). The standard deviation ellipses show each species occupied a unique region within the study area with slight overlaps occurring in some years. Overall, bowhead distribution was oriented along the barrier islands and 20 m isobath on the continental shelf and also included parts of the Barrow Canyon and shelf break that were close to shore (Fig. 8). Gray whale distribution oriented along the Barrow Canyon shelf break near the 50 m isobath; while beluga distribution ellipses centered over Barrow Canyon and offshore slope waters (Fig. 8). This preference for particular depth ranges was similar to that observed during surveys conducted in the 1980's and early 1990's (Clarke et al., 1993; Moore and DeMaster, 1998; Moore et al., 2000). However, ice conditions also appeared to affect bowhead distribution during these earlier years; in particular, heavy ice was associated with whales occupying deeper slope waters (Moore, 2000), which was not a factor during the BOWFEST surveys.

The ROC model examined four specific physical features within the inner box to describe preferred habitat for all three species. For bowhead whales, distance from shore and distance from the shelf break were significant in predicting the presence of bowhead whales ($p < 0.01$, Table 8); therefore, their preferred habitat in-

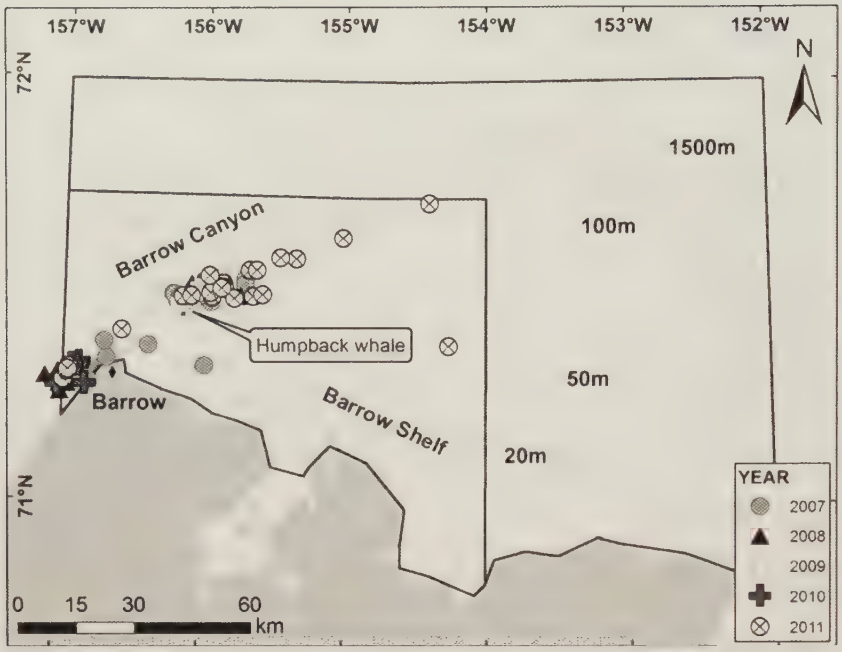

Figure 4.—Locations of a humpback whale and gray whale sightings during BOWFEST aerial surveys from late August to mid-September during the period 2007–11.

Table 4.—Survey days (black boxes) and all on/off trackline bowhead whale sightings and counts (in parentheses) during BOWFEST aerial surveys from late August to mid-September during the period 2007–11. Gray boxes depict days aircraft was available but unable to fly (due to weather or mechanical issues).

	Year				
Day	2007	2008	2009	2010	2011
22-Aug					
23-Aug	10 (59)				
24-Aug	6 (9)				
25-Aug					
26-Aug					0
27-Aug					
28-Aug					
29-Aug		2 (5)			
30-Aug		3 (17)			
31-Aug					
1-Sep				0	
2-Sep			5 (16)		1 (1)
3-Sepr					
4-Sep			9 (21)		
5-Sep		5 (14)			4 (8)
6-Sep	0	23 (103)		7 (33)	
7-Sep	0		5 (5)		0
8-Sep				7 (11)	0
9-Sep	0				4 (17)
10-Sep					
11-Sep	0	9 (11)			
12-Sep				21 (89)	3 (7)
13-Sep		14 (45)		1 (2)	4 (31)
14-Sep			0		2 (4)
15-Sep		0	10 (13)	19 (68)	
16-Sep		0			0
17-Sep				42 (223)	
18-Sep				5 (26)	
Total	16 (68)	56 (195)	29 (55)	102 (452)	18 (68)

cluded the nearshore region oriented east to west that included parts of Barrow Canyon, the shelf break, and Barrow Shelf (Fig. 9). Although these two parameters were significant in determining preferred habitat, the AUC value was 0.67, indicating that the model was only able to correctly discriminate between the presence (bowhead sighting) and absence (random points) 67% of the time. The 0.51 threshold value resulted in approximately 2,576 sq. km of preferred bowhead habitat (38% of the inner box).

All four parameters were significant in predicting gray whale presence ($p < 0.01$, Table 8). Gray whales preferred to be in shallow water that was closer to shore and aligned along the shelf break. A 0.96 value for the AUC indicated that the model was able to correctly classify gray whale presence and absence 96% of the time. The 0.61 threshold value resulted in 802 km^2 of preferred habitat, approximately 12% of the inner box of the BOWFEST study area (Fig. 9).

Of the four parameters included in the model, only bathymetry was significant in predicting beluga whale presence ($p < 0.01$, Table 8). These animals preferred to be in deeper water more than would be predicted at random. An AUC value of 0.82 indicates that the final model correctly discriminated sightings from non-sightings 82% of the time and resulted in 1,948 sq. km of preferred habitat or approximately 29% of the inner box of the BOWFEST study area (Fig. 9), primarily within Barrow Canyon. While there was a large portion of overlap in the predicted habitat for these species, there was clear spatial separation in their preferred habitat (Fig. 8 and 9, last panel).

Behaviors

The behaviors observed most often were swimming or resting at the surface for most species. The only species, other than bowhead whales, observed feeding within the study area was gray whales. Large mud plumes were often listed as the sighting cue for gray whales. Of the bowhead whale

behaviors noted by observers, traveling was reported more often than feeding during most years (45% vs. 22% of all sightings, $n = 221$). Swim direction was noted for 94% of the traveling bowhead whales (Table 9).

Presumably, if the fall migration was underway, most whales would be traveling in a westerly direction (between 226° and 315°T); however, this was not evident in most years (Fig. 10). The sample size in 2007 was too small (only 2 of the 16 sightings noted travel as the primary behavior) to test for significance. In 2008, significantly more bowhead whales traveled in a westerly direction (i.e., about 295°T; Rayleigh's uniformity test probability < 0.05). No significant travel direction was documented in 2009–11.

Aerial observations during the late August to mid-September study period included obvious feeding bouts: observers noted feeding behavior during 7–50% of sightings among the 5 years of the study; and 15–49% of photographed whales exhibited feeding behavior in any given year (Fig. 11). Of the individual whales that were visually or photographically identified as feeding, 81–90%, respectively, were in shelf waters, and the majority of those were clustered around the 20 m isobath (Fig. 12). More feeding behavior was observed and photographed during years when most sightings occurred on the shelf (2007, 2009, 2010) (Fig. 12) but not always in years when bowheads were most abundant (Fig. 13). The lowest percent feeding both visually and photographically occurred in 2008 (Fig. 11), the only year whale swim direction was predominately westerly (Table 9, Fig. 10). Feeding behavior, residency times and site fidelity, and age classes of bowhead whales present within the study area were further explored through the photographic component of BOWFEST.

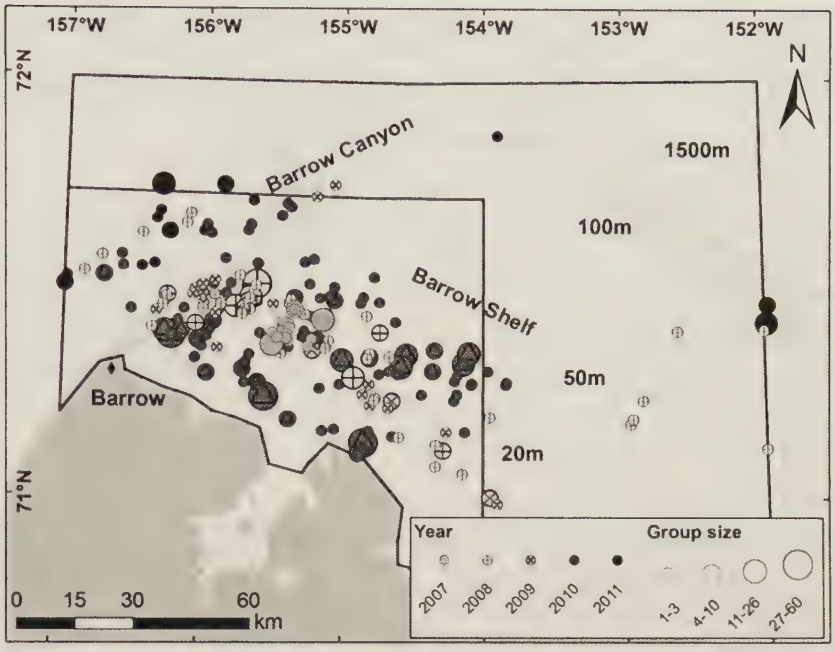

Figure 5.—Locations and group sizes of bowhead whales during BOWFEST aerial surveys from late August to mid-September during the period 2007–11.

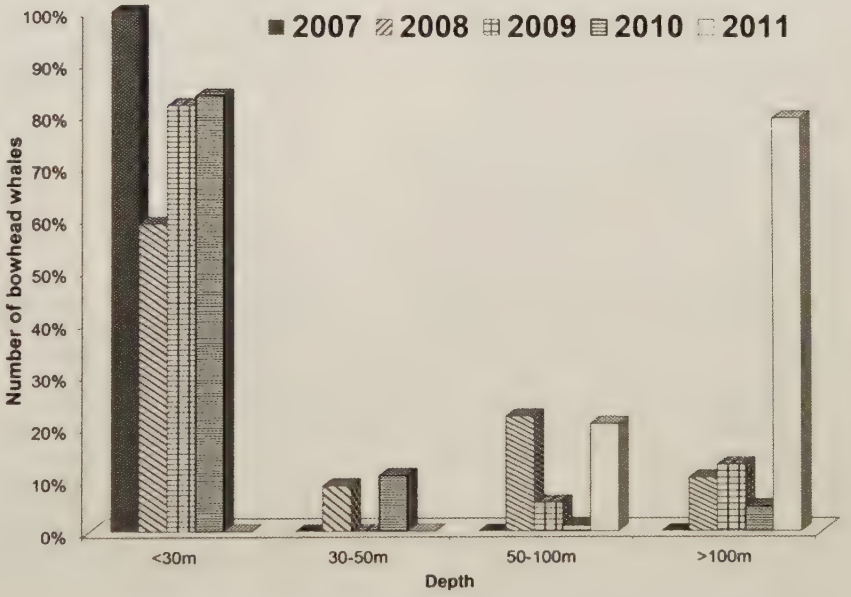

Figure 6.—Depths at which bowhead whales were seen (using counts obtained after departing the trackline to circle: Table 3) during BOWFEST aerial surveys from late August to mid September for the period 2007–11.

Photographic Effort

Bowhead whales were photographed on 22 survey days across the five field seasons. In total, 16.7 hours were spent photographing bowhead whales, resulting in 1,605 pictures taken when

whales were directly beneath the aircraft. Quality ratings of bowhead images indicate that 206 (15%) were of excellent quality (1+ or 1-) in at least one zone on the body (rostrum, midback, lower back, or flukes), 527 (37 %) were good (2+ or 2-) in at least one zone on the body, and 682 (48 %) were not useful (3) in all zones on the body. Photos were considered inadequate usually when a whale was too deep in the water, there was too much splash over the whale's dorsal surface, or the whale was not lying prone in the water.

The 1,605 photographs contained 2,387 images of bowhead whales. Matching and removing duplicate photos from passes left a working set of 1,415 images from which 664 unique whales were identified. Among the 1,415 images used for matching, 33 images (2%) were highly marked (H+ or H-) in at least one zone on the body, 43 images (3%) were moderately marked (M+ or M-) in at least one zone on the body, 667 (47%) were unmarked (U+ or U-) in at least one zone on the body, and 672 (48%) were useless (X) in all zones on the body.

In addition to whale images, 5.5 flight hours were spent taking photographs of calibration targets. Measured images of the floating targets showed a strong correlation between the digital imagery and true lengths from the targets, indicating that radar altimeter performance does not change significantly whether over land or water (Mocklin et al., 2010). Of the 803 images measured for the photogrammetric length (age) class analysis, 654 were within grades 1–6 (Koski et al., 2006).

Bowhead whale images were categorized as feeding (n = 232, 35% of the sample) when mud was present on the whales' dorsal surface, mouths were open (skim feeding), mud plumes were apparent, or whales defecated (fecal plumes). During all years of the aerial study, muddy whales were photographed (Fig. 11). Mocklin et al. (2012) determined that mud can persist for over 4 hours on the skin of a bowhead whale (based

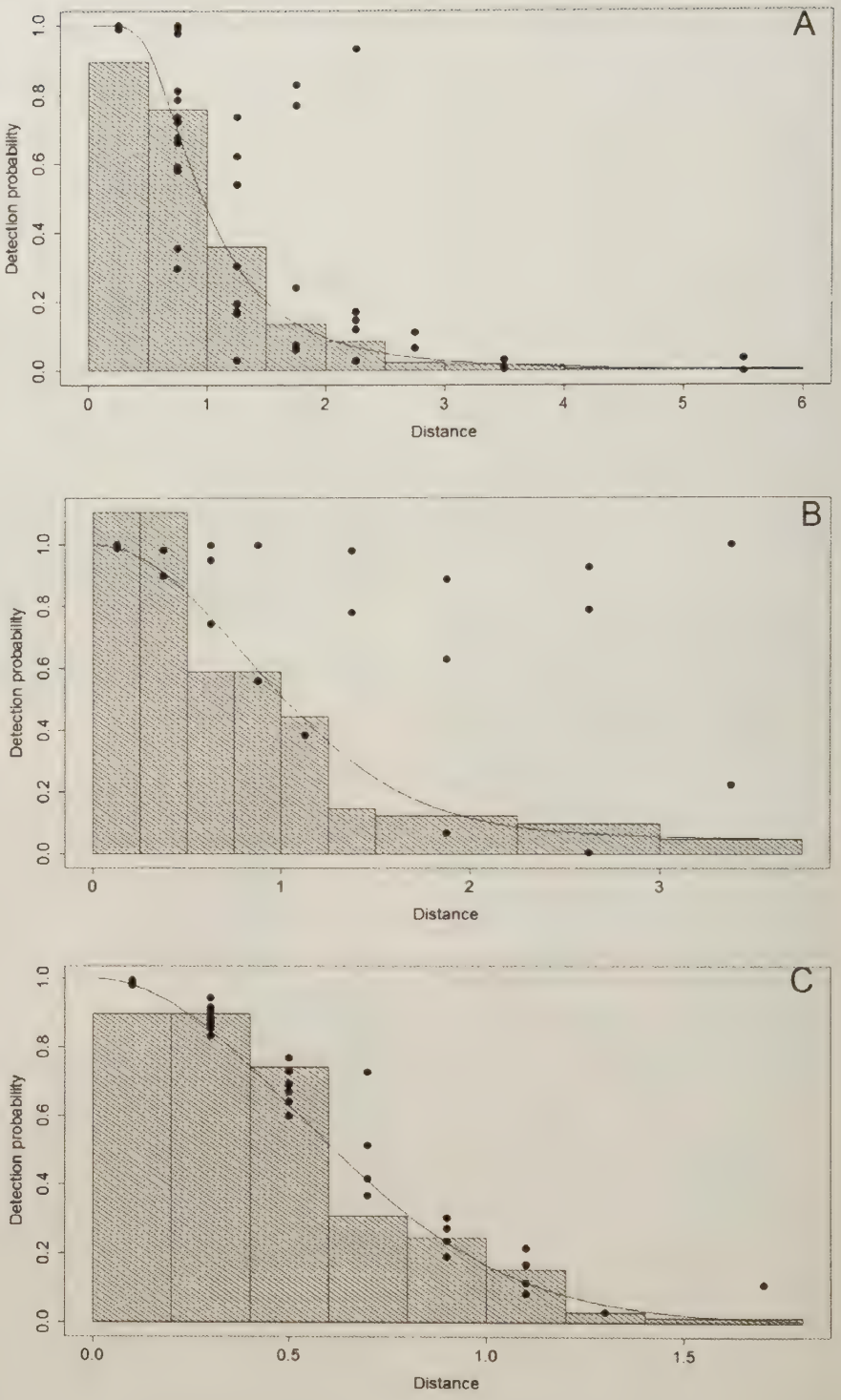

Figure 7.— Histograms of perpendicular distance (km) and fitted detection functions for best-fit model selected by Akaike's Information Criteria (dots represent detection probability for each individual sighting) for (A) bowhead whales, (B) gray whales, and (C) beluga whales during BOWFEST aerial surveys from late August to mid-September for the period 2007–11.

on photo-recaptures), and potentially up to 9 hours or more (based on flow tank tests), depending on swim speed and location on the body. The authors concluded that a whale swimming at 3 km/hr could have been muddied 27 km away from its current location. Even if muddied 27 km away, 90% of the whales photographed during BOWFEST would still be within the boundaries of the inner box of the study area (Fig. 12b). An open mouth, however, suggests active feeding at the current location. This behavior was observed in all years but 2008 (Fig. 11).

Table 5.—Best-fit model proposed to fit perpendicular distance data for bowhead, gray, and beluga whales during BOWFEST aerial surveys from late August to mid-September for the period 2007–11. Summary of model selection for well-supported models with Akaike's Information Criteria (ΔAIC ≤ 2) compared to the best-fit model. Models: hz = hazard rate and hn = half normal. Covariates: beaufort = Beaufort sea state, size.sqrt = square root of group size, obs = observer, glare = glare present or absent, sky = sky condition, w_i = Akaike weight, *P* = average detection probability, and *CV* = coefficient of variation of the average detection probability.

Model, covariates	AIC	ΔAIC	w_i	Parameters	*P*	*CV*
Bowhead whales						
hz, size.sqrt + obs	551.69	0.00	0.310	9	0.19	0.09
hz, size.sqrt + obs + glare	552.62	0.93	0.195	10	0.19	0.09
hz, beaufort + size.sqrt + obs	553.54	1.85	0.123	10	0.19	0.09
Gray whales						
hn, size.sqrt	251.82	0.00	0.135	2	0.32	0.08
hn, size.sqrt + sky	252.37	0.55	0.102	5	0.29	0.12
hn, beaufort + size.sqrt	252.75	0.93	0.085	3	0.32	0.10
hn, size.sqrt + obs	253.21	1.39	0.067	4	0.31	0.13
hr, size.sqrt	253.38	1.56	0.062	3	0.31	0.13
hn, size.sqrt + glare	253.60	1.78	0.055	3	0.32	0.09
Beluga whales						
hn, size.sqrt	367.64	0.00	0.184	2	0.37	0.08
hn (no covariates)	368.71	1.06	0.108	1	0.37	0.07
hn, size.sqrt + glare	369.55	1.91	0.071	3	0.37	0.08
hn, beaufort + size.sqrt	369.55	1.91	0.071	3	0.37	0.08

Table 6.—Number of sightings (*n*), encounter rates (ER, #/km), encounter rate coefficient of variation (ER CV), estimated group size (ES), and estimated group size coefficient of variation (ES CV) for bowhead, gray, and beluga whales by year and domain during BOWFEST aerial surveys from late August to mid-September.

	Bowhead whale					Gray whale					Beluga whale				
Year and Domain	*n*	ER	ER CV	ES	ES CV	*n*	ER	ER CV	ES	ES CV	*n*	ER	ER CV	ES	ES CV
2007															
Inner	5	0.0025	0.71	4.60	0.58	9	0.0044	0.43	1.67	0.22	5	0.0025	0.66	1.60	0.37
Outer	0	0	-	0	-	0	0	-	0	-	4	0.0202	0.83	1.50	0.33
Total	5	0.0022	0.71	4.60	0.58	9	0.0040	0.44	1.67	0.22	9	0.0040	0.51	1.56	0.24
2008															
Inner	45	0.0178	0.23	2.47	0.26	4	0.0016	0.61	3.25	0.69	1	0.0004	1.00	1.00	0.00
Outer	5	0.0117	0.60	1.20	0.17	0	0	-	0	-	0	0	-	0	-
Total	50	0.0169	0.22	2.34	0.25	4	0.0014	0.61	3.25	0.69	1	0.0003	1.00	1.00	0.00
2009															
Inner	16	0.0157	0.41	1.31	0.11	1	0.0010	1.00	1.00	0.00	0	0	-	0	-
Outer	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Total	16	0.0157	0.41	1.31	0.11	1	0.0010	1.00	1.00	0.00	0	0	-	0	-
2010															
Inner	71	0.0289	0.20	2.72	0.25	1	0.0004	1.00	1.00	0.00	1	0.0004	0.99	4.00	0.00
Outer	2	0.0053	0.96	1.00	0.00	0	0	-	0	-	0	0	-	0	-
Total	73	0.0257	0.20	2.67	0.25	1	0.0004	1.00	1.00	0.00	1	0.0004	0.99	4.00	0.00
2011															
Inner	6	0.0017	0.45	1.17	0.14	18	0.0051	0.27	1.44	0.14	41	0.0115	0.41	2.12	0.20
Outer	1	0.0017	1.10	1.00	0.00	0	0	-	0	-	18	0.0300	0.74	3.67	0.31
Total	7	0.0017	0.41	1.14	0.12	18	0.0043	0.27	1.44	0.14	59	0.0142	0.35	2.59	0.18

Table 7.—Number of sightings (*n*), estimated density (D, #/km^2), estimated abundance (N), coefficient of variation (CV), and 95% confidence interval (CI) for bowhead, gray, and beluga whales by year and domain during BOWFEST aerial surveys from late August to mid-September.

	Bowhead whale					Gray whale					Beluga whale				
Year and Domain	*n*	D	N	CV	CI	*n*	D	N	CV	CI	*n*	D	N	CV	CI
2007															
Inner	5	0.0035	25	0.82	6-106	9	0.0022	16	0.45	7-37	5	0.0029	21	0.76	5-83
Outer	0	0	0	0	0-0	0	0	0	0	0-0	4	0.0231	280	0.90	43-1,832
Total	5	0.0013	25	0.82	6-106	9	0.0008	16	0.45	7-37	9	0.0155	302	0.84	51-1,778
2008															
Inner	45	0.0138	100	0.35	51-196	4	0.0011	8	0.69	2-28	1	0.0003	2	1.00	0-12
Outer	5	0.0062	75	0.70	19-299	0	0	0	0	0-0	0	0	0	0	0-0
Total	50	0.0090	176	0.36	85-364	4	0.0004	8	0.69	2-28	1	0.0001	2	1.00	0-12
2009															
Inner	16	0.0083	60	0.36	30-123	1	0.0005	4	1.01	1-20	0	0	0	0	0-0
Outer	-	-	-	-	-	-	-	-	-	-	-				
Total	16	0.0083	60	0.36	30-123	1	0.0005	4	1.01	1-20	0	0	0	0	0-0
2010															
Inner	71	0.0255	185	0.30	103-335	1	0.0002	1	1.01	0-8	1	0.0011	8	0.99	2-43
Outer	2	0.0023	27	0.97	3-218	0	0	0	0	0-0	0	0	0	0	0-0
Total	73	0.0110	213	0.30	120-379	1	0.00008	1	1.01	0-8	1	0.0004	8	0.99	2-43
2011															
Inner	6	0.0011	8	0.55	3-22	18	0.0025	18	0.28	10-31	41	0.0169	123	0.43	54-280
Outer	1	0.0012	14	1.18	2-131	0	0	0	0	0-0	18	0.0679	825	0.75	150-4,530
Total	7	0.0011	22	0.80	4-111	18	0.0009	18	0.28	10-31	59	0.0112	948	0.66	208-4,320

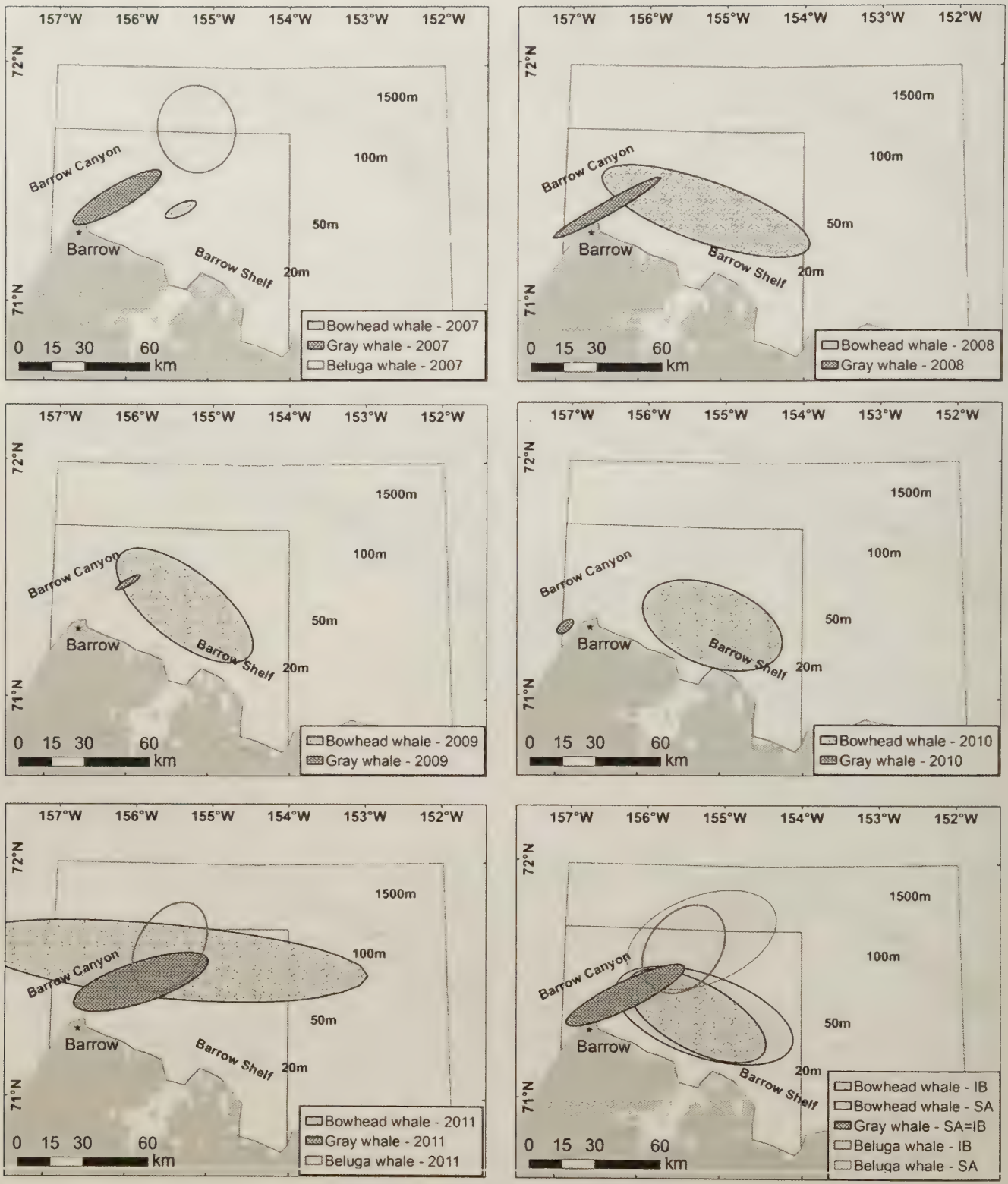

Figure 8.—Standard deviation ellipses (capturing approximately 68% of sightings weighted by group size) showing the regions occupied by bowhead, gray, and beluga whales during BOWFEST aerial surveys from late August to mid-September during the period 2007–11. Beluga sample sizes were too small during the period 2008–2010 to create ellipses. Given increased effort in the inner box (IB), the same analyses were run using only sightings within this region to confirm inner box distributions were not significantly different from sightings in the entire study area (SA) for all years combined (last panel).

Table 8.—Logistic regression and ROC model results: final model parameters; AIC scores; AUC and threshold values; habitat preference areas; and the proportion of habitat in the inner box (IB) of the BOWFEST study area for bowhead, gray, and beluga whales.

Whale type	Model parameters	k	AIC	AUC	Threshold	Habitat area (km²)	Percent of IB
Bowhead	DISTSHORE + DISTSHELF	2	532.39	0.67	0.51	2575.81	37.96
Gray	BATHY+SLOPE+DISTSHORE+DISTSHELF	4	137.81	0.96	0.61	801.64	11.81
Beluga	BATHY	1	107.14	0.82	0.40	1947.94	28.71

Table 9.—Bowhead whales observed traveling within the BOWFEST aerial survey study area from late August to mid-September during the period 2007–11. (Note: sample size was too small in 2007).

Year	Sightings headed westerly (226°-315°)	Total "travel" sightings with headings	Percent heading westerly	Rayleigh's uniformity test (KCS, 2012)	Grand mean vector
2007		2	–		
2008	12	21	57.1%	$Z = 7.103$, $p = 4.82E\text{-}4$	294.774°
2009	4	8	50.0%	$Z = 1.672$, $p = 0.192$	
2010	16	52	30.8%	$Z = 0.414$, $p = 0.661$	
2011	6	12	50.0%	$Z = 1.130$, $p = 0.33$	
Total	38	93	40.9%		

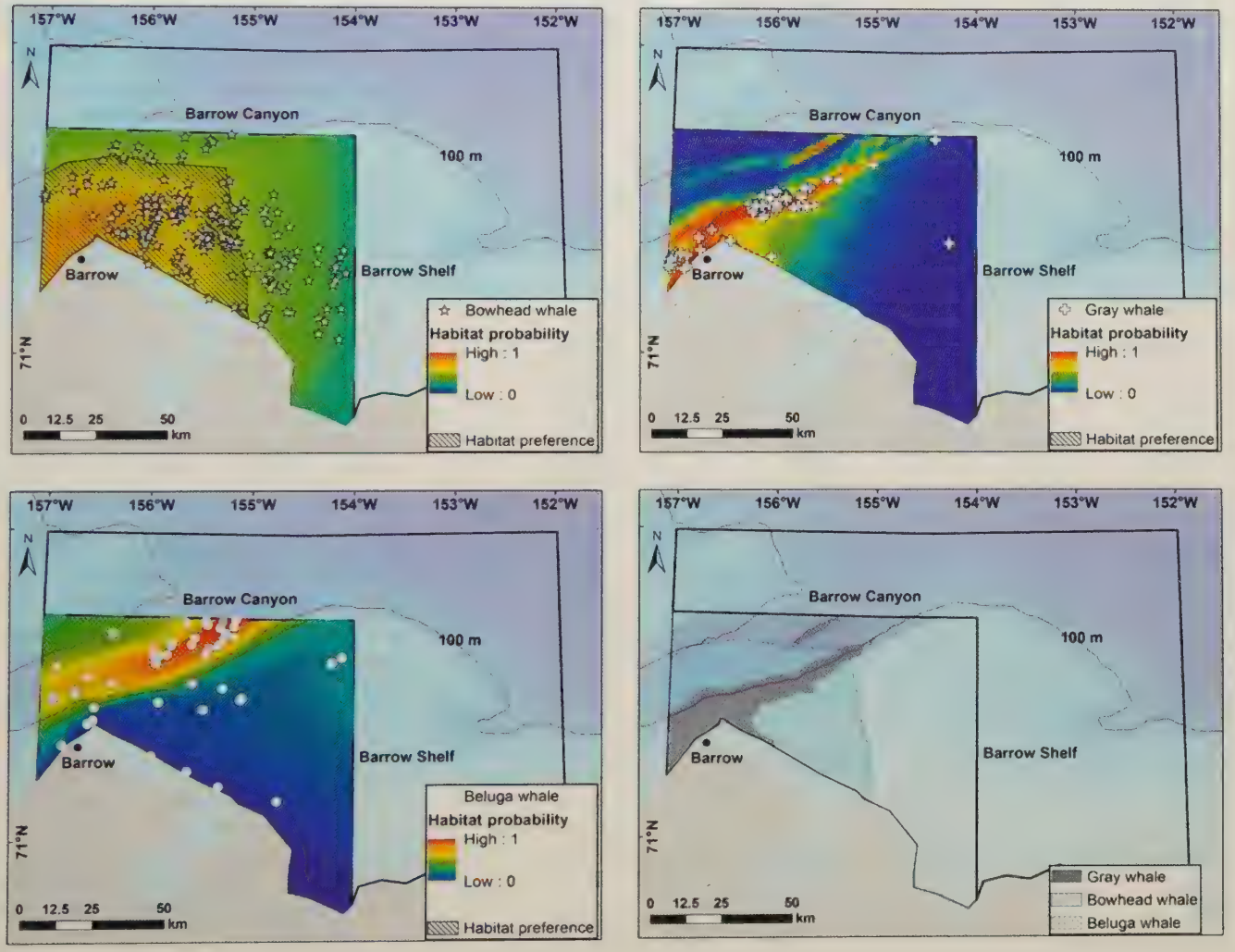

Figure 9.—Late summer habitat probability (low/blue to high/red) and preference (black cross-hatch) for bowhead (stars), gray (crosses), and beluga (circles) whales near Barrow, Alaska, based on sightings within the inner box of the BOWFEST study area collected during late August to mid-September during the period 2007–11. Habitat preferences for all three species are shown in the last panel.

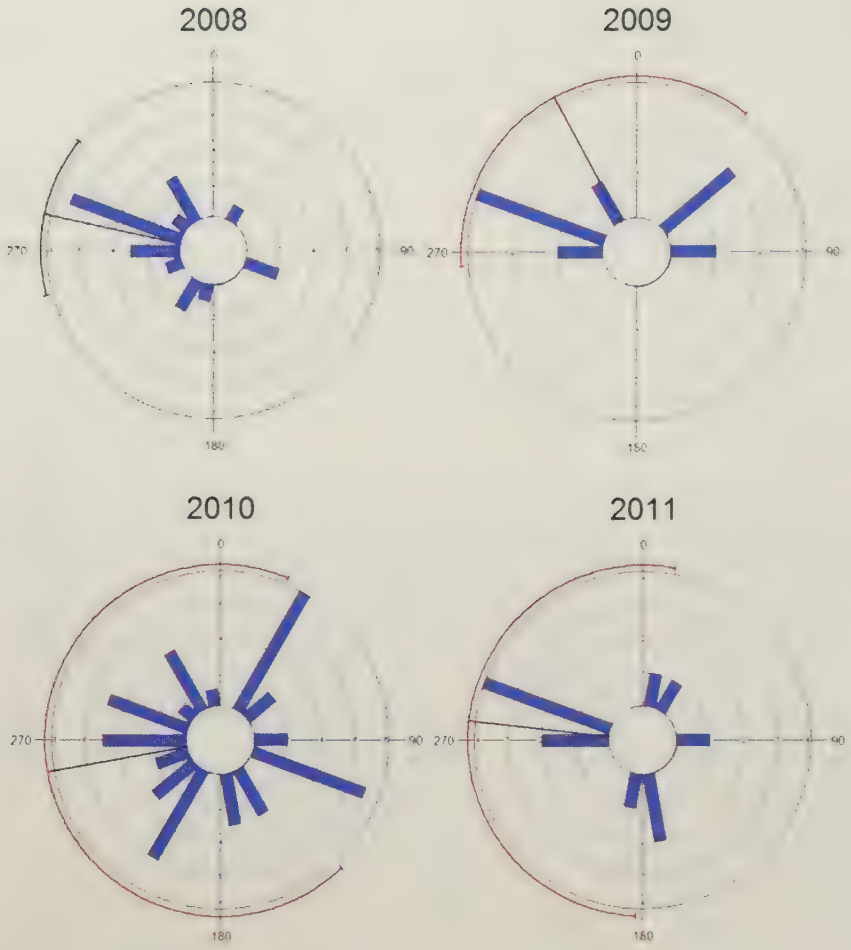

Figure 10.—Swim directions of bowhead whales observed during BOWFEST aerial surveys from late August to mid-September during the period 2008–11 (Note: sample size was too small in 2007). Only 2008 showed a significant clustering of sightings in any direction (black line as opposed to red lines in other years).

During the aerial survey in 2010, groups of bowhead whales were observed with open mouths swimming in echelon formation, and in an unusual position on their sides instead of upright (Fish et al., 2013). Echelon formation had been documented before for bowhead whales, but usually whales were upright (Würsig and Clark, 1993; George et al.[6]), though a lone whale skim feeding on its side was photographed in 2006 in the BOWFEST study area (Moore et al. 2010a). Moore et al. (2010a) also described "head lunging" bowhead whales observed on two occasions in 2006, a behavior not observed during the BOWFEST aerial surveys. A fecal plume was evident on only one occasion during the BOWFEST study (Fig. 11).

Residency Times and Site Fidelity

Among the 664 unique whale images, there were only three resightings of bowhead whales on different days within a study year (Fig. 14). These intrayear sightings occurred in 2009 (n = 1) and 2011 (n = 2). None of the whales had moved west of their initial sighting location as would be expected if they were migrating past Barrow. The whale photographed two days later in 2009 remained along the 20 m isobath, while the whales photographed five days later in 2011 had separated, but both remained in deeper waters (>100 m), one in Barrow Canyon and the other at the easternmost border of the study area (Fig. 14). The individual that remained in Barrow Canyon was the only intrayear-matched whale that appeared to have been feeding (fecal plume evident in the photograph taken on 9/9/2011).

There were three resightings of bowhead whales among the 5 years of BOWFEST photographs (Fig. 14). These interyear sightings included one whale photographed in 2007 and 2009, one in 2007 and 2011, and one in 2008 and 2010. Two of these whales were resighted along the 20 m isobath, near their initial sighting location two years earlier (Fig. 14). The third whale was first observed near the 20 m isobath but 5 years later was photographed in deep water (>100m) on the easternmost boundary of the study area (Fig. 14). Both whales observed in 2007 appeared to be feeding (mud on rostrums), but only the whale resighted in 2009 had evidence of feeding (mud on the rostrum). Mud was also on the rostrum of the whale observed again in 2010, but there was no evidence of feeding in the 2008 image.

In 2011, the bowhead aerial abundance spring survey (BAASS) flew in the Barrow area photographing whales from April to June (Mocklin et al.[13]). While analyses still continue on this dataset, a match between this dataset and BOWFEST included one bowhead whale mother with calf photographed in May and September (Fig. 14 and 15). Both sightings occurred over deep water (>100 m); at the easternmost border of the study area in the spring and in Barrow Canyon in late summer (Fig. 14). The mother had mud on her chin and tip of her rostrum in the photograph taken during the spring mi-

[13]Mocklin, J., J. C. George, M. Ferguson, L. Vate Brattström, V. Beaver, B. Rone, C. Christman, A. Brower, B. Shea, C. Accardo. 2012. Aerial photography of bowhead whales near Barrow, Alaska, during the 2011 spring migration. Pap. SC/64/BRG3 pres. to IWC Sci. Committee, May 2012, 9 p.

gration (possible evidence of feeding behavior) (Fig. 15A).

Age Classes

Using photogrammetric lengths, bowhead whales were sorted into specific age classes: calf, juvenile, and adult (Fig. 16). Of the 654 images of sufficient quality to obtain length measurements (prior to matching), 65% were juveniles (between 6 and 13 m), 35% were adults (>13 m), and 1% were calves (<6 m). While there was no statistical difference between percentages of juveniles and adults during the study period (paired t-test; $p = 0.15$), three of the 5 years (2008, 2010, 2011) included large numbers of younger juveniles in the photographic sample. Rugh (1990) noted that because young whales have fewer scars, which accumulate as bowheads age, these whales may go unrecognized, and therefore, unmatched. Of 213 images classified as juveniles and assigned a unique whale number, only 6 (3%) were highly marked and 12 (6%) were moderately marked in at least one zone on the body. This likely contributed to the low number of photographic resightings during the BOWFEST study period.

Obtaining adequate lengths for feeding whales proved to be difficult. Image quality ratings for 276 feeding whales (including within day, intrayear, and interyear matches) were a 3 (i.e., not useful) for all zones of the body for 157 (58%) of these images. Lengths were obtained for about 34% of whales identified as feeding (Table 10). Of these, 46% were juveniles and 54% were adults.

Conclusions

The aerial survey component of BOWFEST was designed to docu-

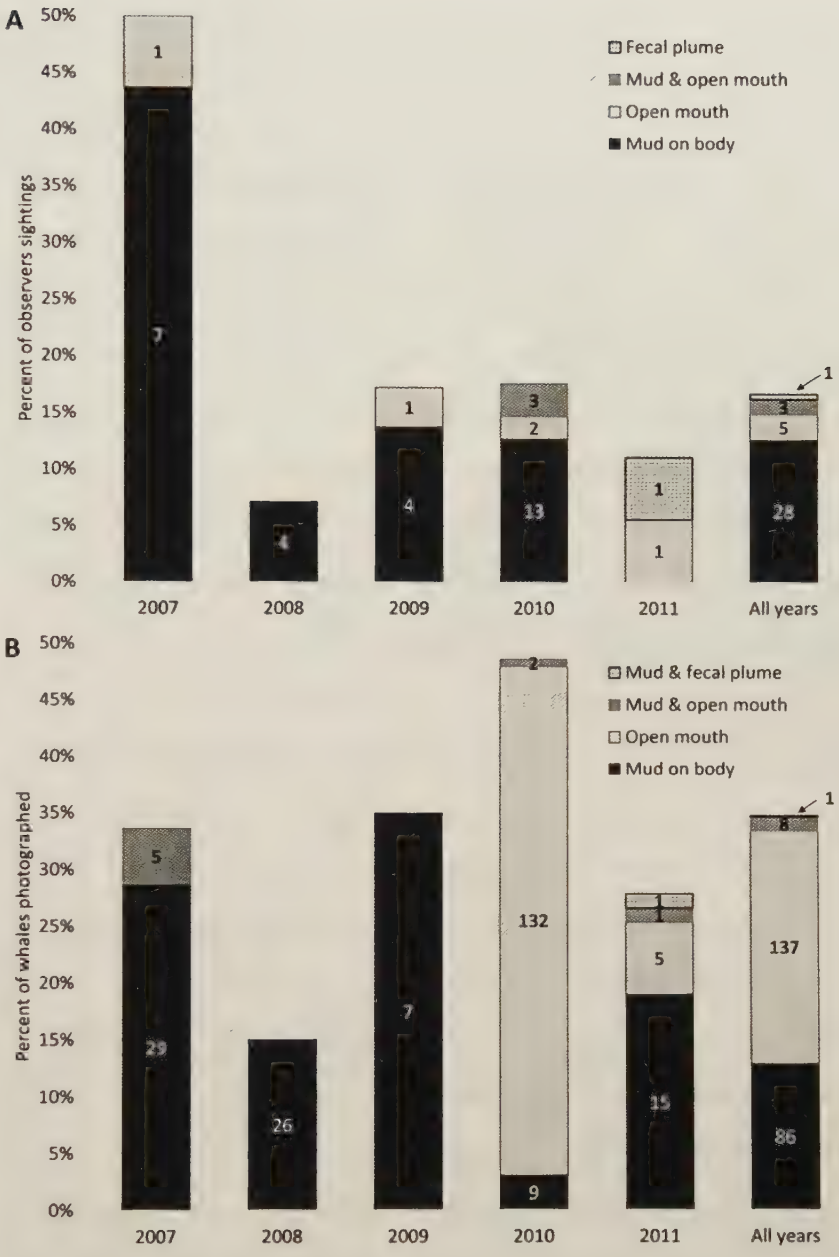

Figure 11.—Percentage of bowhead whales (A) observed and (B) photographed displaying feeding behaviors during BOWFEST aerial surveys from late August to mid-September for the period 2007–11. Sample sizes are noted within each column.

Table 10.—Bowhead whales observed feeding within the BOWFEST aerial survey study area from late August to mid-September during the period 2007–11. Lengths (when available) were binned in meter increments.

	Juveniles (6–<13m)						Adults (>13m)					
Year	7–<8	8–<9	9–<10	10–<11	11–<12	12–<13	13–<14	14–<15	15–<16	16–<17	17–<18	No length
2007					2		6	13		3	2	8
2008		1	2	4	4	1	3	3	1			7
2009								1				6
2010	1	1	2	1	5							133
2011			1	2	4	5	7	1	2			
Total	1	2	5	7	15	6	16	18	3	3	2	154

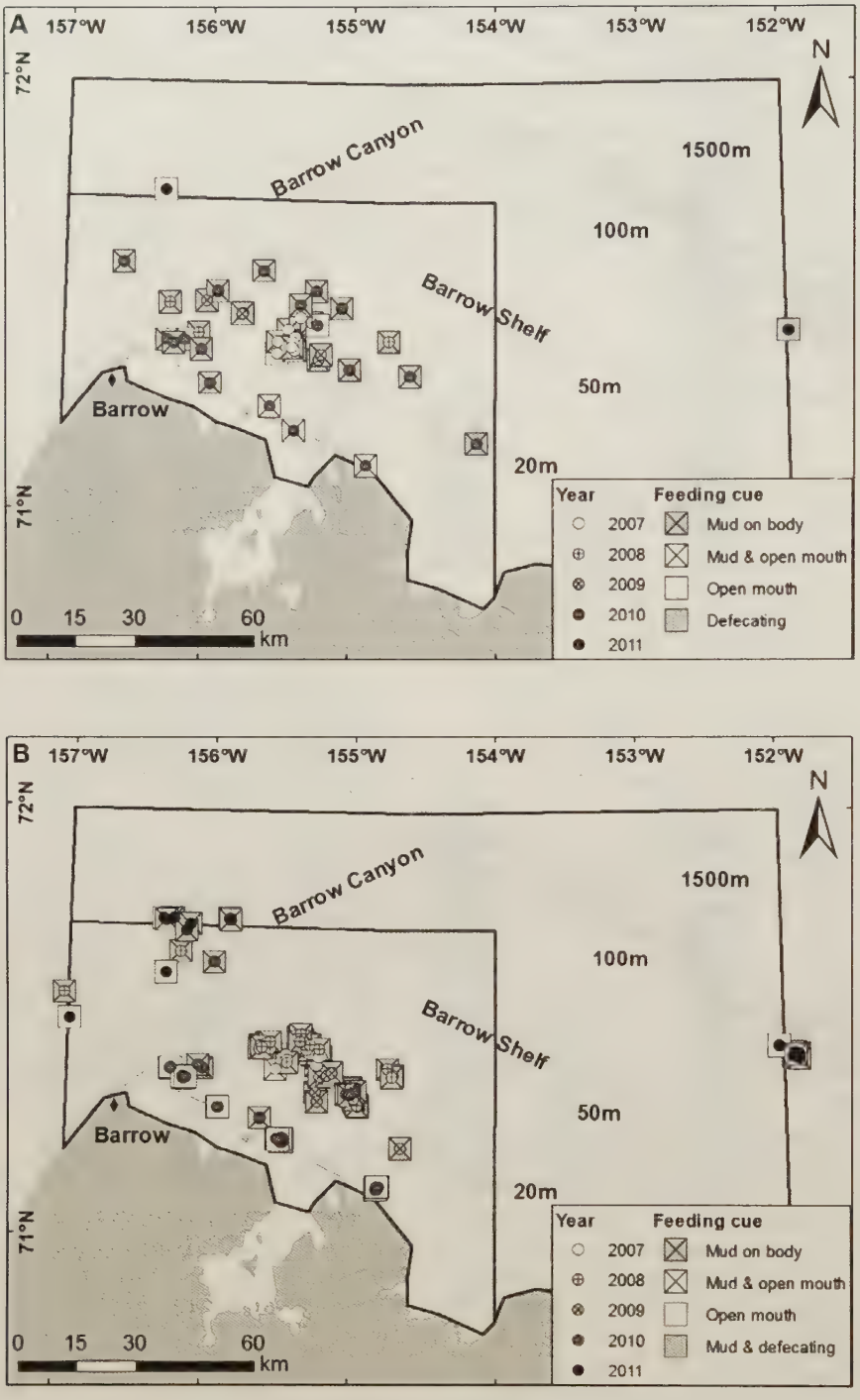

Figure 12.—Locations of feeding bowhead whales (A) observed and (B) photographed during BOWFEST aerial surveys from late August to mid-September for the period 2007–11.

ment patterns and variability in the timing and distribution of bowhead whales and to provide an estimate of temporal and spatial habitat use near Barrow, Alaska. Abundance estimates during this time period ranged from 22 (*CV* 0.80) to 213 (*CV* 0.30) bowhead whales within the combined study areas. Traveling was the most commonly recorded behavior, but swim direction was highly variable among years, suggesting bowhead whales were not migrating through the area during the survey period. Only in 2008 was swim direction significantly clustered around a mean and clearly westward. This also coincided with the lowest percentage of whales photographed feeding during the study period, and the only year when skim feeding was not observed or photographed.

Most bowhead whales were located in shelf waters < 30 m deep when feeding behaviors were observed (81%) or photographed (90%). Habitat partitioning was evident among the cetacean species observed in greatest numbers: bowhead, gray, and beluga whales. Bowhead distribution aligned close to shore, extending from within Barrow Canyon on the western boundary of the study area toward the eastern edge, running along the 20 m isobath in almost all years. Gray whales aligned along the shelf break near Barrow in all years, while belugas, when present, were primarily offshore over submarine canyon waters. This patterning among species was consistent with partitioning observed on a much larger scale across the Beaufort and Chukchi seas (e.g., Clarke et al., 2016). When modeling habitat preferences based on all survey years, four parameters were considered: bathymetry, bathymetric slope, distance from shore, and distance from the shelf break. Both distance from shore and distance from the shelf break were significant in predicting the presence of bowhead whales. All four parameters were significant in predicting gray whale presence. Only bathymetry was significant in predicting beluga whale presence.

Although the paucity of individual

bowhead whale resightings between survey days suggested very low residence times, we found the photogrammetric sample was largely comprised of juveniles. Young whales typically are unmarked and, therefore, not matched. Only one instance of feeding was documented among the intrayear matches (6 images total) though the whales remained within the BOWFEST study area. The across season match of a mother with calf had evidence of feeding during the spring but not late summer. Among the interyear matches, 4 of the 6 images documented feeding behaviors for each whale that was re-identified.

It appears that some whales return to the region after initially heading west into the Chukchi Sea during what would be considered the migratory period. Quakenbush et al. (2010) performed a kernel density analysis of tagged whale movements that showed, in September, the area with the highest probability of use was northeast of Barrow. Their satellite tag data also showed that bowhead whales do not move across the Beaufort Sea in a continuous stream. Three of the 19 tagged whales left the Barrow area heading west, only to return and spend 13–32 days in the waters off Barrow (Quakenbush et al., 2010). All of our intrayear matched whales moved east of their original sighting location, which was not expected so close to the westbound fall migration.

Aggregations of bowhead whales have been linked to wind speeds and directions that in association with shelf and coastal currents, retain and concentrate their prey on the shelf near Barrow (Ashjian et al., 2010; Okkonen et al., 2011). Although, bowheads were most abundant in the BOWFEST survey area in 2008 and 2010, this did not necessarily mean that whales were feeding. Further analysis of the BOWFEST dataset, in particular the whales displaying feeding behaviors, may provide additional insights.

As the bowhead population continues to grow and "there is no evidence that the population size is above the maximum net productivity level or

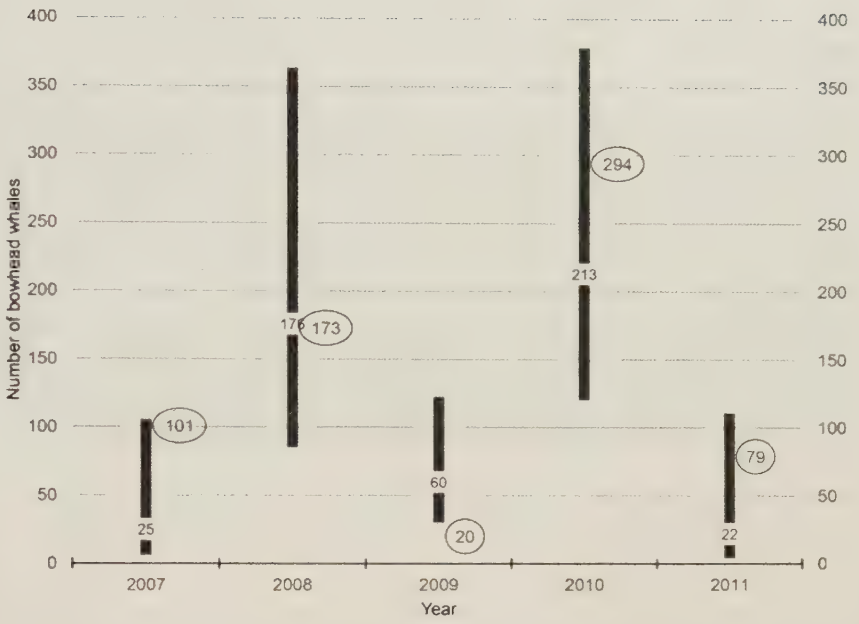

Figure 13.—Annual abundance estimates with associated confidence intervals (black bars) and number of unique bowhead whales photographed (ovals) during BOWFEST aerial surveys from late August to mid-September for the period 2007–11.

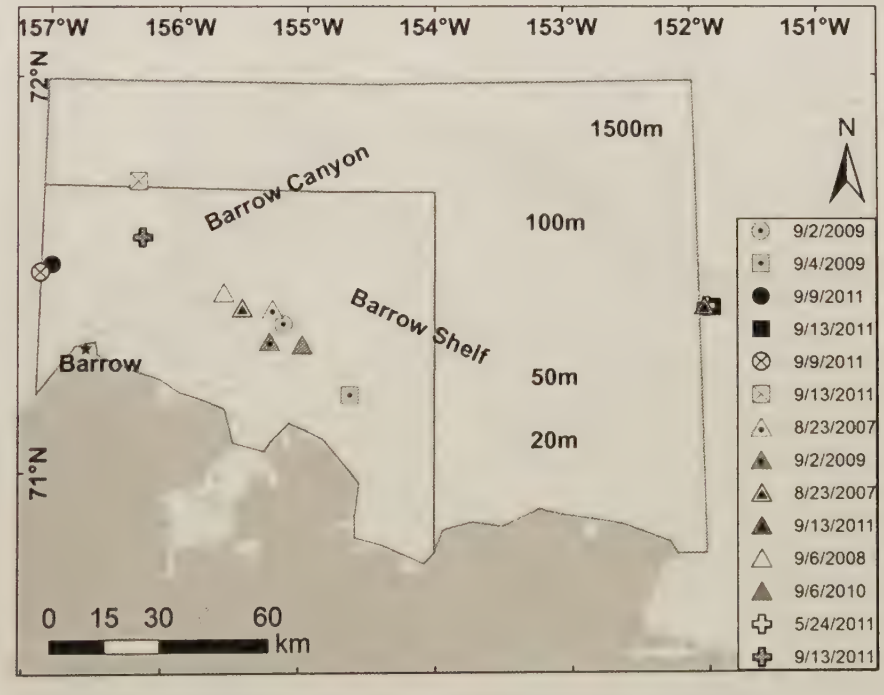

Figure 14.—Locations of bowhead whales with photographic matches. There were three intrayear BOWFEST matches (circle: first sighting; square subsequent), three interyear BOWFEST matches (triangles), and one intrayear match between spring (BAASS survey) to late summer (BOWFEST) (crosses).

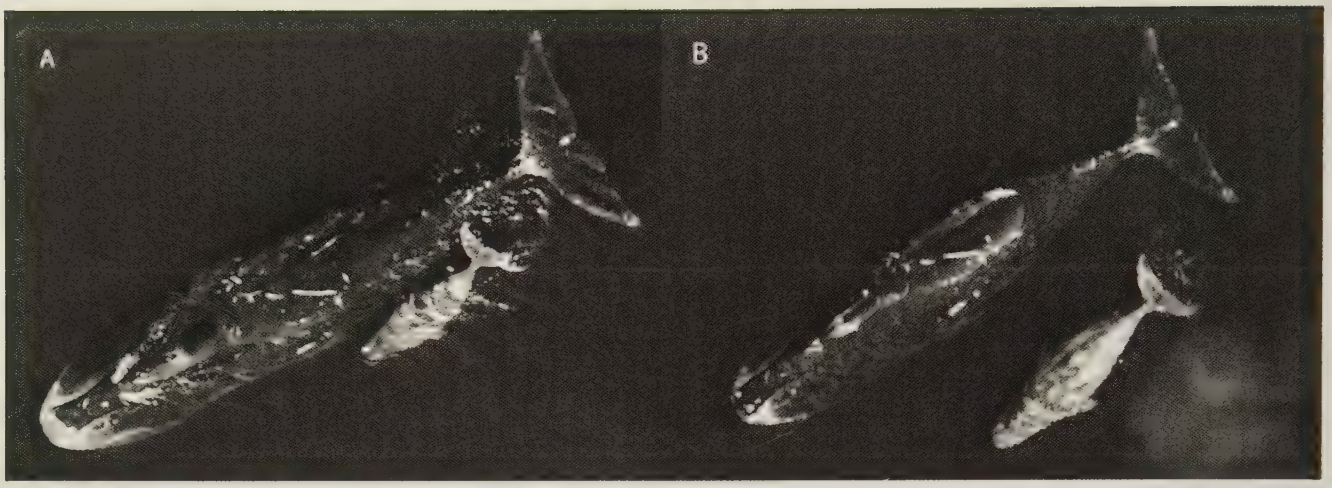

Figure 15.—Intrayear matches of a bowhead whale mother with calf observed (A) during the BAASS aerial survey April–June 2011 and (B) BOWFEST aerial surveys late August to mid-September 2011. Note the change in calf size relative to the adult. The mother had mud on her chin and tip of her rostrum in the spring photograph, possibly indicating feeding behavior.

near carrying capacity" (Givens et al.[14]), more whales may seek foraging opportunities in the western Beaufort and the Chukchi seas in response to increased feeding pressure in the eastern Beaufort Sea foraging areas. Other species have extended their ranges or are showing up in greater numbers in the Chukchi and western Beaufort seas—such as gray whales, humpback whales, fin whales, *Balaenoptera physalus*; minke whales, *B. acutorostrata*; and killer whales (e.g., Clarke et al., 2013). This suggests the potential for increasing prey competition among zooplankton feeders, as well as increased predation by killer whales.

Industrial activity is also expected to increase in the Arctic (Reeves et al., 2012). Although bowhead whales are exposed to oil and gas development activities in the eastern Beaufort Sea and expanding activities (i.e., seismic exploration) in the Chukchi and western Beaufort seas (e.g., Moore et al., 2012), commercial fishing and most shipping operations have not yet reached these regions. These activities will not only affect bowhead whales and other species endemic to the Arctic (Reeves et al., 2014), but potentially species expanding their range into this region. Mitigating the potential impacts on these species from these activities will require putting preemptive measures in place (Moore et al., 2012; Reeves et al., 2012, 2014). The BOWFEST aerial study provides a 5-year record of late summer presence of cetaceans in the western Beaufort Sea, adding to the growing body of

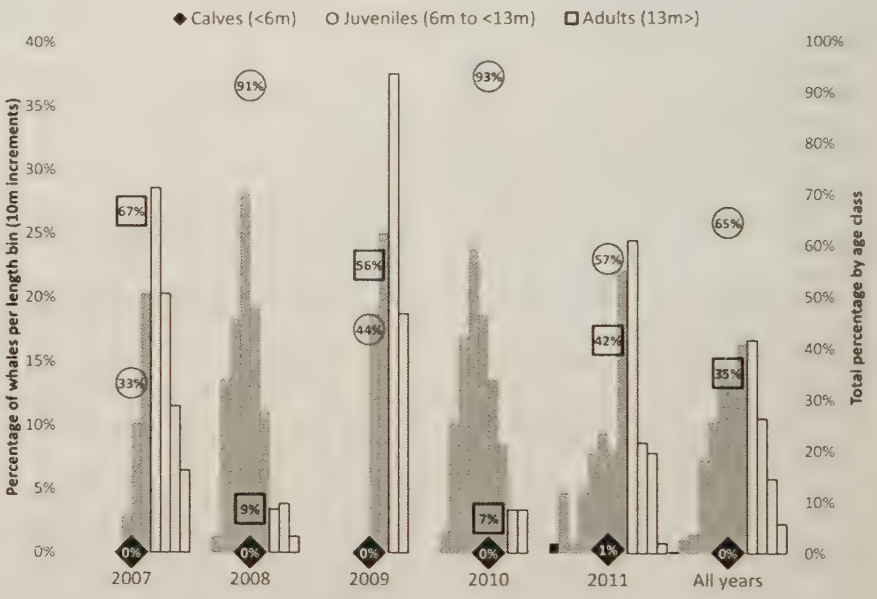

Figure 16.—Age class distribution of bowhead whales during BOWFEST aerial surveys from late August to mid-September for the period 2007–11. Histogram shows percentage of whales per length bin in 10m increments for calves (black columns), juveniles (gray columns), and adults (white columns). Total percentage by age class is shown within each symbol for calves (diamonds), juveniles (circles), and adults (squares).

[14]Givens, G. H., S. L. Edmondson, J. C. George, R. Suydam, R. A. Charif, A. Rahaman, D. Hawthorne, B. Tudor, R. A. DeLong, and C. W. Clark. 2013. Estimate of 2011 abundance of the Bering-Chukchi-Beaufort Seas bowhead whale population. Pap. SC/65a/BRG1 pres. to IWC Sci. Committee, May 2013, 30 p.

knowledge of these species and their habitat preferences in a region undergoing rapid change.

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NOAA's Aircraft Operation Center provided the aircraft and crew. Our pilots were Jason Mansour, Wally Pierce, and Nicole Cabana in 2007; Nicholas Toth and Jon French in 2008; Nicholas Toth and Chris Daniels in 2009; Brad Fritzler and Rob Mitchell in 2010; and Brad Fritzler and Francisco Fuenmayor in 2011. These pilots filled a critical role in keeping the aircraft at the preferred altitude while flying intricate patterns over moving whales. Ron Pauley, Mike Merek, and Rob Militic provided mechanical support for the aircraft through these years. Dee Allen flew with us one day in 2009 (assisting with video photography) and Christy Sims joined the team in 2011.

Wayne Perryman loaned us a radar altimeter and provided technical advice, and Don LeRoi loaned us the FMC mount and assisted with the camera mount installation. Craig George provided the land calibration target. Noah Lawrence-Slavas assisted with the design of the water-borne target used in 2008–09, and Frederick Brower and Catherine Berchok towed this floating target array within the survey area. Janet Clarke provided the statistics and figure for the bowhead swim direction analysis and Rayleigh test. Alex Zerbini consulted on the distance sampling analysis. This study was conducted under MMPA Scientific Research Permit No. 782-1719 (years 2007-10) and Permit No. 14245 (2011).

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From Whaling to Tagging: The Evolution of North Atlantic Humpback Whale Research in the West Indies

AMY S. KENNEDY and PHILLIP J. CLAPHAM

Introduction

The waters surrounding the Greater and Lesser Antilles (otherwise known as the West Indies, Fig. 1) are host to a variety of cetacean species, either seasonally or year-round. These include bottlenose dolphins, *Tursiops truncatus*; spotted dolphins, *Stenella* spp.; beaked whales, Family Ziphiidae; killer whales, *Orcinus orca*; sperm whales, *Physeter macrocephalus*; and humpback whales, *Megaptera novaeangliae* (Mattila et al., 1989; Mattila and Clapham, 1989; Mignucci-Giannoni, 1998; Roden and Mullin, 2000; Gandilhon, 2012).

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North Atlantic humpback whales migrate to the wider Caribbean region, between Cuba and the Caribbean coast of Venezuela, to mate and calve each winter; they originate in a broad range of summer feeding grounds across temperate and high latitudes, ranging from the Gulf of Maine to the Arctic (Mattila et al., 1989; Katona and Beard, 1990; Smith et al., 1999). Although some breeding behaviors (e.g., singing and competitive groups) are observed in northern feeding grounds, the term "breeding ground" is used to describe low-latitude tropical or subtropical wintering areas where reproductive behaviors, such as singing, sexual competition, and nursing, are predominant, and where little to no feeding takes place (Chittleborough, 1965; Clapham et al., 1993; Clapham, 1996; Clark and Clapham, 2004).

Although humpbacks have historically used habitats off both the Greater (northern) and Lesser (southern) Antilles (Fig. 1) as winter breeding grounds, a comparison of modern sighting data to whaling records indicates that the latter region is currently host to a lower density of whales than was apparent in the 19th century (Winn et al., 1975; Reeves et al., 2001; Swartz et al., 2003). Today, the largest concentrations of breeding humpbacks are seen on Silver, Navidad, and Mouchoir Banks (north of Hispaniola), as well as in Samaná Bay in the northeastern Dominican Republic (DR). While a population shift from the southeastern to the northern West Indies has been proposed (Reeves et al., 2001), historical records suggest that the lack of 19th century whaling records from Dominican waters relates more to an inability of the whalers to obtain the necessary licenses than to an absence of whales in this region.[1]

Humpback whales wintering in the wider Caribbean region, and especially those on Silver Bank, comprise one of the most intensely studied large whale populations in the world (Figures 2, 3, and 4 provide an overview of the projects discussed in this review). Modern scientific research on Antillean humpbacks began in the late 1960's, and researchers have subsequently worked to establish overall abundance estimates and to describe the spatial and temporal distribution, habitat preference, migration, mating behavior, acoustic repertoire, population identity, and genetic structure for the North Atlantic population.

In addition to short-term, local studies, two large-scale studies, Years of the North Atlantic Humpback or YONAH, conducted in 1992–93) (Smith et al., 1999), and More of the North

ABSTRACT—North Atlantic humpback whales, Megaptera novaeangliae, *migrate from summer feeding grounds across the temperate and high latitudes to breeding grounds in the West Indies each winter. Humpbacks over-wintering near the Antillean islands comprise one of the most intensely studied populations of large whales in the world. Since scientific research began there in the late 1960's, researchers have worked to describe humpback distribution, abundance, and behavior in this major North Atlantic breeding ground. The progression and advancement of research techniques used in this region are largely representative of humpback studies worldwide. While decades of line-transect, photographic identification, acoustic, and genetic research have given us a good understanding of the occurrence and distribution of humpbacks in much of the West Indies, gaps in our knowledge still exist. This review describes the humpback whale research methods used throughout the West Indies that have evolved over time, from whaling data collection to modern day satellite telemetry, and summarizes the resultant knowledge regarding humpback distribution, abundance, and behavior. For conservation efforts within marine sanctuaries to effectively safe-guard the population, increased multi-national research and collaboration is needed to protect the North Atlantic humpback population from threats encountered throughout its entire life cycle.*

[1]Bonnelly, Idelisa. Fundación Dominicana de Estudios Marinos (FUNDEMAR), Calle Sócrates Nolasco No. 6, Residencial Carla Pamela, Apartamento 401 Ensanche Naco, Santo Domingo, D.R., personal comm., 01 April 2008.

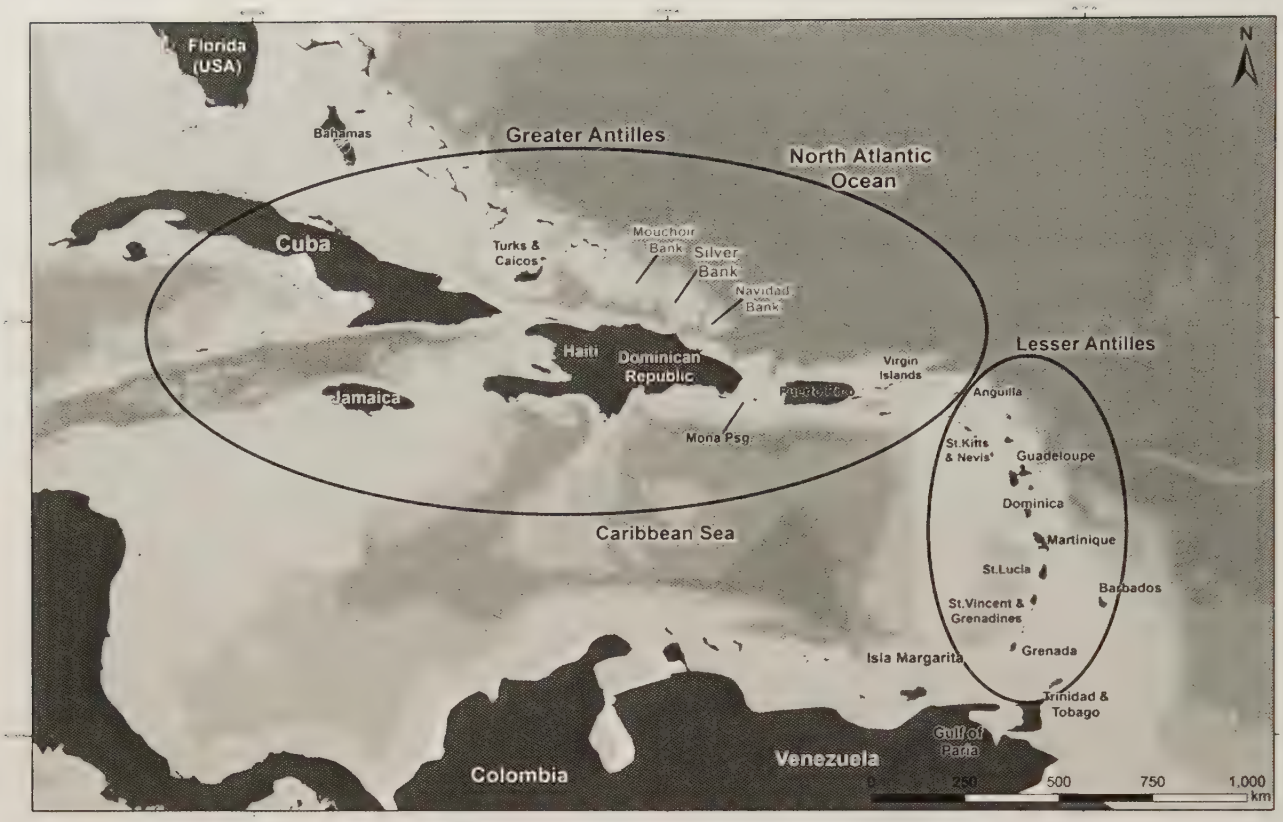


Figure 1.—The Greater and Lesser Antilles and Caribbean coast of Venezuela.

Atlantic Humpbacks or MONAH, conducted in 2004–05) (Clapham et al., 2005), were undertaken to address the need for reliable abundance estimates of North Atlantic humpback whales. As a result of several decades of research throughout the Antillean Islands, much is now known about humpback whales in this region and in the broader ocean basin. Nonetheless, some aspects of the biology and structure of this population remain poorly understood.

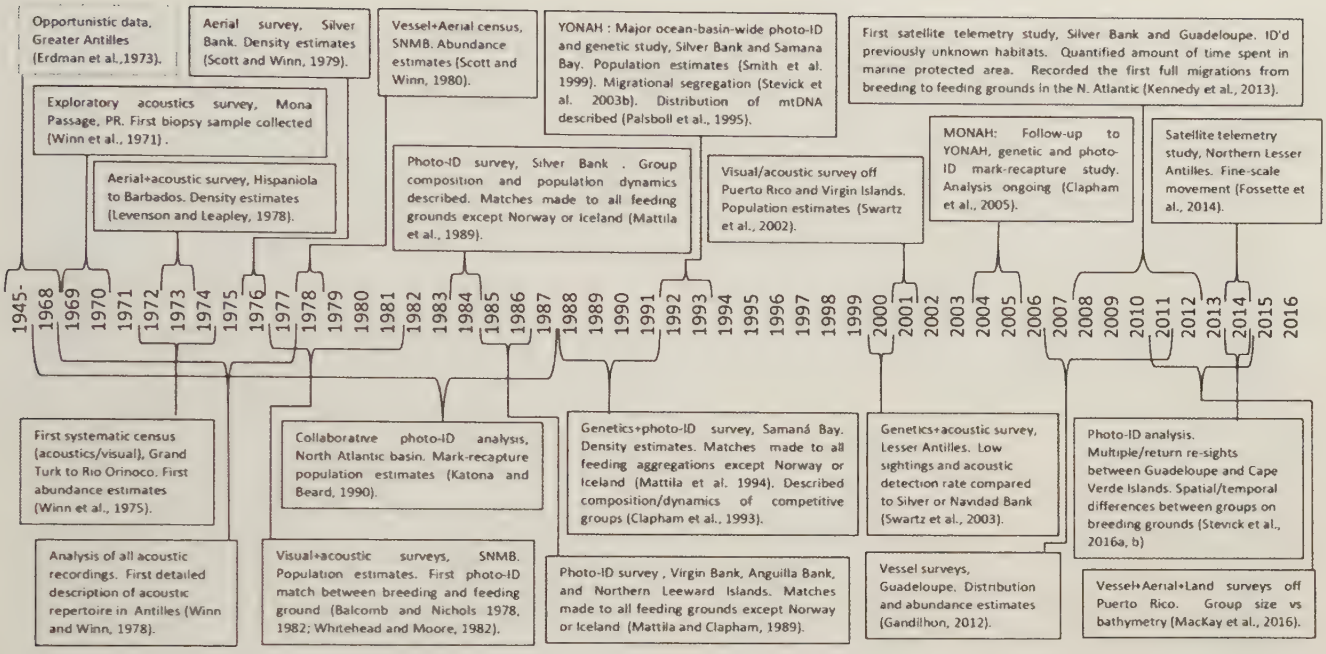
This review chronicles the evolution of scientific research methods, from the review of historical whaling data to present-day telemetry work, that have been employed throughout the major North Atlantic humpback breeding grounds. Additionally, we will discuss our current gaps in knowledge about the population and suggest future research strategies that may fill in those gaps. Finally, we include a discussion about the significance of this area to the status and management of the overall North Atlantic humpback whale population.

Methods

Whaling Research

The most basic form of whale research is the visual survey. Simple documentation of time, position, and number of whales seen in a particular area often represents the basis for all forthcoming scientific research to expand upon. In essence, whalers collected the first visual survey data when they recorded the date, time, and position of a whale sighting or kill. Consequently, much of what we know about the historical occurrence of humpback whales in various parts of the world comes from whaling logbooks and journals, and many modern genetic, acoustic, photographic identification (photo-ID), and telemetry studies have been designed around historical whaling records of sightings and/or catch distribution.

Commercial exploitation of humpbacks in the West Indies began in the 1820's with whaling by vessels from the great "Yankee" whale fishery. Sailing vessels from New England (notably from Provincetown, Mass.) "humpbacked" in the West Indies, either as a primary occupation or as part of broader expeditions targeting sperm whales, *Physeter macrocephalus,* elsewhere in the North Atlantic (Townsend, 1935; Mitchell and Reeves, 1983; Reeves et al., 2001; Smith and Reeves, 2002; Smith and Reeves, 2003a, b). During the sail-based Yankee whaling era, demand for humpback-derived products peaked between 1850 and 1890, and an estimated 1,617 humpback whales were killed in the West Indies during that time (Smith and Reeves, 2003b). Whaling logbook data from 19th century American whalers show that the


Opportunistic data, Greater Antilles (Erdman et al.,1973).
Aerial survey, Silver Bank. Density estimates (Scott and Winn, 1979).
Vessel+Aerial census, SNMB. Abundance estimates (Scott and Winn, 1980).
YONAH : Major ocean-basin-wide photo-ID and genetic study, Silver Bank and Samana Bay. Population estimates (Smith et al. 1999). Migrational segregation (Stevick et al. 2003b). Distribution of mtDNA described (Palsboll et al., 1995).
First satellite telemetry study, Silver Bank and Guadeloupe. ID'd previously unknown habitats. Quantified amount of time spent in marine protected area. Recorded the first full migrations from breeding to feeding grounds in the N. Atlantic (Kennedy et al., 2013).
Exploratory acoustics survey, Mona Passage, PR. First biopsy sample collected (Winn et al., 1971).
MONAH: Follow-up to YONAH, genetic and photo-ID mark-recapture study. Analysis ongoing (Clapham et al., 2005).
Satellite telemetry study, Northern Lesser Antilles. Fine-scale movement (Fossette et al., 2014).
Aerial+acoustic survey, Hispaniola to Barbados. Density estimates (Levenson and Leapley, 1978).
Photo-ID survey, Silver Bank . Group composition and population dynamics described. Matches made to all feeding grounds except Norway or Iceland (Mattila et al., 1989).
Visual/acoustic survey off Puerto Rico and Virgin Islands. Population estimates (Swartz et al., 2002).
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First systematic census (acoustics/visual), Grand Turk to Rio Orinoco. First abundance estimates (Winn et al., 1975).
Collaborative photo-ID analysis, North Atlantic basin. Mark-recapture population estimates (Katona and Beard, 1990).
Genetics+photo-ID survey, Samaná Bay. Density estimates. Matches made to all feeding aggregations except Norway or Iceland (Mattila et al. 1994). Described composition/dynamics of competitive groups (Clapham et al., 1993).
Genetics+acoustic survey, Lesser Antilles. Low sightings and acoustic detection rate compared to Silver or Navidad Bank (Swartz et al., 2003).
Photo-ID analysis. Multiple/return re-sights between Guadeloupe and Cape Verde Islands. Spatial/temporal differences between groups on breeding grounds (Stevick et al., 2016a, b)
Analysis of all acoustic recordings. First detailed description of acoustic repertoire in Antilles (Winn and Winn, 1978).
Visual+acoustic surveys, SNMB. Population estimates. First photo-ID match between breeding and feeding ground (Balcomb and Nichols 1978, 1982; Whitehead and Moore, 1982).
Photo-ID survey , Virgin Bank, Anguilla Bank, and Northern Leeward Islands. Matches made to all feeding grounds except Norway or Iceland (Mattila and Clapham, 1989).
Vessel surveys, Guadeloupe. Distribution and abundance estimates (Gandilhon, 2012).
Vessel+Aerial+Land surveys off Puerto Rico. Group size vs bathymetry (MacKay et al., 2016).

Figure 2.—Timeline of humpback whale research conducted off the Greater and Lesser Antilles.

highest catches of humpbacks during the winter breeding season occurred from the Windward Islands to Trinidad and westward along the Venezuelan coast (the Spanish Main) between January and May (Townsend, 1935; Mitchell and Reeves, 1983; Price, 1985; Smith and Reeves, 2003a, b).

The shore-based killing of whales by Antilleans was rare until the 1860's. The first permanent humpback whaling station was established in Barbados in 1867 (Mitchell and Reeves, 1983). After the establishment of the Barbados station (which killed an estimated 233 humpbacks between 1869 and 1878), shore-based whaling spread throughout the Windward Islands and Trinidad.

Although detailed records were not kept, an estimated average of 44 whales per year were killed by shore-based whalers between 1880 and 1913 (Mitchell and Reeves, 1983). Most of these stations had shut down by 1880, but at least 5 were still operational in 1913, between St. Vincent and Grenada (Mitchell and Reeves, 1983; Smith and Reeves, 2002). The St. Vincent hunt, a native operation that until recently employed traditional Yankee whaling methods, continues at a low level today from the island of Bequia.

Reeves et al. (2001) analyzed a subsample of logbooks from Yankee whaling vessels from 1823 to 1889 (initially compiled by Mitchell and Reeves, 1983) to further describe the location and number of humpback whales killed or observed by the sail-based whaling fleet in the breeding grounds. Their detailed analysis describes the extensive "humpbacking" effort undertaken in the French West Indies (Guadeloupe, St. Lucia, St. Vincent), the Grenadines, Trinidad and Tobago, and the Gulf of Paria (Venezuela). In particular, the highest number of whales "taken, struck or seen" in the 19th century occurred in St. Vincent and the Grenadines (≈958 whales), followed by Guadeloupe (≈592), Venezuela (≈216), and Dominica/Martinique/St. Lucia (≈193) (Reeves et al., 2001). Approximately 167 whales were "taken, struck or seen" off the DR, yet more than a third of those records come from one voyage in the late 1800's. Records of catches from Samaná Bay and Puerto Rico were rare (Reeves et al., 2001), but so are records of vessels operating there at all.

The occurrence of relatively high humpback densities along the Lesser Antilles and Caribbean coast of Venezuela in the late 1800's stands in sharp contrast to the observed density of humpbacks observed in this region today. After a survey of the Greater and Lesser Antilles, Winn et al. (1975) estimated that 85% of the North Atlantic humpback breeding population is seen on the banks north of Hispaniola. In terms of density, the estimates of 1.15 whales/km^2 (Balcomb and Nichols, 1982) and 1.13 whales/km^2 (Whitehead and Moore, 1982) on Silver Bank are significantly higher than estimates for Samaná Bay (0.17 whales/km^2; Mattila et al., 1994), Virgin Bank (0.044 whales/km^2; Mattila and Clapham, 1989), and 0.005 whales/km^2 on the "upper chain" (includes Puerto Rico, Virgin Bank, and Anguilla Bank) (Winn et al., 1975). The most recent confirmation of low humpback densities outside the Greater Antilles were reported by Swartz et al. (2003), who saw only 31 whales (between Guadeloupe and Trinidad/

Figure 3.—Rough outlines of large-scale humpback whale research projects carried out from the late 1960's to present day off the Greater and Lesser Antilles.

Tobago) over nearly 3,200 km of effort in the eastern and southeastern Antilles in February and March of 2000. In addition to those sightings, there were acoustic detections of singing humpbacks throughout the Lesser Antilles between St. Croix and Isla Margarita, yet group size and/or population density cannot be estimated from sonobuoy data (Swartz et al., 2003).

Reeves et al. (2001) suggested that the apparent paucity of historical records of whaling effort in the Greater Antilles indicated that humpback whales were not utilizing the area extensively until the 20th century, and thus the modern abundance of humpbacks in the waters around Hispaniola was a post-whaling phenomenon. The authors suggested that this shift in humpback whale distribution from the Lesser to the Greater Antilles after the late 1800's was due to overexploitation in the breeding and/or feeding grounds throughout the North Atlantic (Winn and Scott, 1977; Reeves et al., 2001).

However, subsequent examination of non-whaling historical documents by researchers with the Centro de Investigatión de Biología Marina (CIBIMA) at the Autonomous University of Santo Domingo has provided evidence that the waters of Hispaniola were always host to abundant whales (almost certainly humpbacks).[1] Documents from France show that they, together with the United States and the United Kingdom, offered to recognize the sovereign status of the newly independent (in 1844) Dominican Republic in exchange for permission to hunt the abundant whales in those waters; Samaná Bay is specifically mentioned in some of these sources.[1] Notes about "abundant" whales in archived historical documents suggest that Dominican waters have long represented an important humpback habitat and that the absence of whaling records from this area was more likely related to a failure by whaling vessels to obtain required national licenses.

Regardless of whether the current densities of whales on Silver, Navidad, and Mouchoir Banks during the breeding season are a recent phenomenon, the high densities of humpbacks in the Lesser Antilles that are apparent from 19th century catch records stand in sharp contrast to current observations. The reason for this disparity in distribution is unknown, as is the question of why the Lesser Antilles have not been significantly repopulated since commercial whaling ceased in 1927 in the West Indies and in 1955 throughout the North Atlantic. The possibility that whales from the Lesser Antilles represent an entirely separate breeding population from those to the northwest seems unlikely given that photo-ID matches have linked both

Figure 4. –Rough outlines of small-scale humpback whale research projects carried out from the late 1960's to present day off the Greater and Lesser Antilles.

areas to the same western North Atlantic feeding grounds (Stevick et al., 1999b; Robbins et al., 2006), yet new research suggests that this separation may be more significant than previously thought.

Modern Scientific Research

Although there had been some opportunistic humpback observations in the West Indies beginning in the mid-1940's (Erdman et al., 1973), modern studies of humpback whales in the West Indies began in the 1960's and continue today; Figure 2 provides a timeline of the development of this research. From the late 1960's to the early 1980's, humpback whale research was primarily based upon aerial and shipboard visual line-transect and acoustic survey methods. These were used to establish abundance, distribution, habitat use, and overall humpback whale movements.

In the 1970's, the discovery that humpback whales could be individually identified by the unique pattern of markings on the ventral surface of the tail (Katona et al., 1979; Katona and Whitehead, 1981) inspired the inception of a variety of short- and long-term studies of humpback whales in the West Indies and also in various summer feeding grounds in the higher-latitude North Atlantic, as well as elsewhere in the species' global range (Clapham, 1996).

Humpback whale research in the Antilles effectively began with a brief exploratory acoustics survey conducted in Mona Passage (Puerto Rico) in 1969 (Winn et al., 1971). After this, Winn et al. (1975) led the first systematic shipboard survey for humpback whales, from Grand Turk (Turks and Caicos) to Rio Orinoco (Venezuela) in the winters of 1972 and 1973. This study combined passive acoustics with visual surveys. The authors estimated that 85% of the humpback whales in the West Indies breeding grounds were found in the Silver, Navidad, and Mouchoir Banks complex, and the high calf density there indicated that these areas were critically important breeding and calving grounds.

At about the same time as the Winn et al. (1975) study, the Naval Ocean Research and Development Activity (NORDA) conducted an aircraft-based acoustic survey from Hispaniola to Barbados in January of 1973 (Levenson and Leapley, 1978). Scott and Winn (1980) conducted shipboard and aerial visual surveys of Silver and Navidad Banks two years later to compare and inter-calibrate the two survey techniques, and to further document the size, distribution, movement, and stock identity of North Atlantic humpback whales in the Dominican breeding grounds.

Also in the late 1970's, George Nichols initiated an annual research program using the 144-ft barquentine *Regina Maris*. From this platform, Balcomb and Nichols (1978, 1982) and Whitehead and Moore (1982) conducted visual and acoustic surveys in the winters of 1976 to 1981, from the Gulf of Paria (Venezuela) to Puerto Rico. As with previous surveys, the only large concentrations of humpbacks were found on Silver and Navidad Banks, with peak sightings made at the end of January for Navidad Bank, and two weeks later for Silver Bank.

David Mattila and colleagues began a humpback study in Mona Passage off the western coast of Puerto Rico in 1978, and collected photo-ID data and song recordings there for the next six winters. The results of this study remain largely unpublished, although selected results were given in Mattila and Clapham (1989), and individual identification photographs from Puerto Rico have been widely used in publications resulting from the North Atlantic Humpback Whale Catalogue (NAHWC, curated and published by the College of the Atlantic in Bar Harbor, Maine). In 1984, Mattila et al. (1989) conducted a six-week photo-ID survey of Silver Bank to further address the scope of genetic mixing of feeding stocks on the breeding ground. In the following two years (1985, 1986), Mattila and Clapham (1989) conducted the first surveys of Virgin Bank, Anguilla Bank, and the northern Leeward Islands using similar techniques.

Herbert Hays and Howard Winn observed a number of humpback whales during a short visit to Samaná Bay in the northeastern DR in the late 1970's (unpub. data), but formal research did not begin there until CIBIMA researchers collaborated with the Center for Coastal Studies, in Massachusetts, in 1987 to conduct the first exploratory survey of the bay. This expedition led to a series of annual vessel surveys between 1988 and 1991. During the latter study, Mattila et al. (1994) used photo-ID to describe the occurrence, population composition, and habitat use by humpback whales in Samaná Bay, and the relationship of this bay to the more populous offshore banks.

The collection of identification photographs from the entire North Atlantic resulted in a growing catalogue of humpback fluke photos. This permitted the first connections to be made among breeding and feeding areas (Balcomb and Nichols, 1978). Furthermore, by the late 1980's, the NAHWC was large enough (n=3,647 individuals) to allow researchers to employ a photo-ID mark-recapture abundance estimate technique originally suggested by Balcomb and Nichols (1978) (Katona and Beard, 1990).

By the late 1980's, existing abundance estimates were outdated and it was apparent that they suffered from bias relating to use of different survey methods. Furthermore, there had been little sampling in the central and eastern North Atlantic (notably Iceland and Norway). To address these problems, the first ocean-basin-wide photographic and biopsy survey, YONAH, was conducted in 1992 and 1993 (Smith et al., 1999). Researchers from seven countries, from the West Indies to Norway, employed standardized sampling methods and demonstrated that a study on such a broad spatial scale, while expensive and logistically complex, can produce a more reliable and comprehensive and less biased dataset than multiple small-scale surveys conducted over many years. YONAH has subsequently been seen as a model for other large-scale studies, notably the Structure of Populations Levels of Abundance and Status of Humpbacks (SPLASH) project in the North Pacific (Barlow et al., 2011).

Although the Lesser Antilles had been sporadically studied by earlier expeditions (Winn et al., 1975; Balcomb and Nichols, 1978; Levenson and Leapley, 1978), most effort had been focused in the major areas of concentration in the northern West Indies; far less was known about the distribution and occurrence of humpbacks in the Windward Islands and areas to the south. To address this deficiency, in February and March of 2000, Swartz et al. (2003) undertook a visual, genetic, and acoustic survey in the Lesser Antilles to describe the regional abundance of humpback whales in areas with lower densities than the Greater Antilles, and to determine the feasibility of using acoustic methods to detect and locate whales. The survey covered the Leeward Islands (except for the Virgin Islands, the islands of Anguilla Bank, and St. Eustatius), the Windward Islands, Barbados, Trinidad and Tobago, and the northern coast and offshore islands of Venezuela.

One year later, Swartz et al. (2002) conducted another survey to determine the winter distribution and abundance of cetaceans in the waters surrounding the Bahamas, Turks and Caicos, Puerto Rico, and the U.S. and British Virgin Islands. Between 2008 and 2011, Gandilhon (2012) conducted systematic line-transect studies for all cetaceans, including humpbacks, using the waters around Guadeloupe. Most recently, MacKay et al. (2016) conducted vessel, aerial, and land-based surveys for humpback whales off western Puerto Rico between 2011 and 2014 and described habitat preferences based on group size in that area.

By 2004, the estimates of abundance produced by YONAH were more than 10 years old and there was interest by the U.S. government in conducting a further review of North Atlantic humpback status relative to the U.S. Endangered Species Act. Consequently, a follow-up study to YONAH, called More of the North Atlantic Humpback (MONAH), was initiated. The goal of MONAH was to obtain humpback abundance estimates using biopsy-based genetic mark-recapture methods, although photo-ID data were also collected as a secondary objective.

In recent years, satellite telemetry has become a powerful tool used to describe the fine-scale movements of large whales (Baumgartner and Mate, 2005; Heide-Jørgensen et al., 2006; Zerbini et al., 2006). Kennedy et al. (2013) conducted the first North Atlantic humpback telemetry project

between 2008 and 2012. Fine-scale individual movement data, as well as the first documented migrations from breeding to feeding grounds, were recorded. A second satellite telemetry project was conducted in April of 2014 from Anguilla that revealed movement throughout the French West Indies and Virgin Islands (Fossette et al., 2014).

Results

Distribution and Abundance

The Winn et al. (1975) systematic shipboard survey of the Antilles generated the first North Atlantic humpback population estimate of 785–1,157 (CI, presumed 95%) animals. Average density estimates of 0.21 whales/km^2 (Silver Bank) and 0.23 whales/km^2 (Navidad Bank) were also calculated; these densities demonstrated that the great majority of breeding whales in the West Indies were spending time in the Silver, Navidad, and Mouchoir Banks complex.

Levenson and Leapley's (1978) aircraft-based acoustic survey in 1973 deployed 82 passive acoustic sonobuoys and recorded visual observations along the predetermined flight track. All but one of the acoustic detections from NORDA's sonobuoys occurred east of longitude 70°W and north of latitude 16°N, with the highest concentrations centered over Silver and Navidad Banks.

In 1976, Scott and Winn (1979) conducted two additional aerial survey flights over Silver Bank to explore the utility of using different methods (including photogrammetry) for humpback whale stock assessment. The authors calculated a density of 0.311 ± 0.069 (95% CI) whales/km^2. Since this density was statistically similar to the Winn et al. (1975) calculation, despite an estimated growth rate of 5% per year (from ACMRR, 1976), Scott and Winn (1979) concluded that vertical photographic sampling methods are cost-effective and efficient, yet the precisions of the resulting estimates may be low.

Scott and Winn's (1980) 1978 surveys calculated an abundance estimate of 1,069–1,377 (95% CI) on Silver Bank and 306–370 (95% CI) whales on Navidad Bank. The density estimates from this study (0.513 whales/km^2, sd = 0.36) for Silver Bank and 0.554 whales/km^2, sd = 0.368) for Navidad Bank were over 50% higher than the corrected estimate calculated by Winn et al. (1975). If this difference was due strictly to population growth, this would equate to an 8.5% annual population increase between 1972 and 1978; however, differences in sampling methods and/or temporal coverage may have contributed to the observed density increase. Additionally, Scott and Winn's (1980) comparison of census techniques found that detection probability during aerial surveys was particularly sensitive to environmental state, and shipboard survey estimates should be considered more accurate, particularly if they include photo-ID.

The sighting data collected in 1977 from *Regina Maris* did not account for detection parameters, yet crude population estimates were reported (Table 1). The estimates derived from the 1977 survey roughly equated to a 1.8% population increase per year from the Winn et al. estimate (1975), yet the authors admit that their number did not account for all potential recruitment and/or sampling bias.

Sighting data collected from *Regina Maris* in 1980 and 1981 were ranked and sorted on detection probability parameters and produced, in theory, more accurate mean population estimates for Silver, Navidad, and Mouchoir Banks, yet there were still sampling method and/or analysis biases that needed to be addressed (Balcomb and Nichols, 1982). While the authors tentatively compared their results to prior estimates, it was clear that bias from differing survey methods and vastly different spatial and temporal coverage among breeding ground censuses would preclude reliable analyses of population trends (Table 1).

Elsewhere in the West Indies breeding range, Mattila and Clapham's 1985–86 surveys found that humpback sightings peaked in mid- to late-February on Virgin Bank and Anguilla Bank, with an overall mean of 0.044 whales/nmi^2 (sd = 0.029) on Virgin Bank. The density of humpbacks on Anguilla Bank was approximately 50–66% lower than either Virgin Bank or Puerto Rico. The seasonal density shifts and within-season photo-ID matches documented in this and other papers (e.g., Balcomb and Nichols, 1982) suggested a northeast-to-southwest movement through the Antilles during the winter.

Table 1.—Differing mean population estimates for Silver and Navidad Banks, 1973, 1977, 1980, 1981.

	Mean Population Estimates	
Year	Silver Bank	Navidad Bank
1973[1]	754	110
1977[2]	809	96
1980[3]	1432	441
1981[3]	963	214

[1]Winn et al., 1975.
[2]Balcomb and Nichols, 1978.
[3]Balcomb and Nichols, 1982.

In Samaná Bay, Mattila et al. (1994) discovered that whale density (0.17 whales/km^2) in that area was an order of magnitude lower than on Silver or Navidad Banks, but higher than in Mona Passage (Puerto Rico) or on Virgin Bank. Again, a general trend toward peak abundance in February was noted, but this varied slightly among years.

Using the NAHWC collection of 3,647 individual whales, Katona and Beard (1990) conducted a mark-recapture analysis using all available humpback photos taken between 1952 and 1987 to calculate an overall population estimate of 5,505 ± 2,617 (95% CI) animals, and an unweighted mean population estimate of 3,776 ± 4,853 (95% CI) whales on the Silver, Navidad, and Mouchoir Banks complex. Katona and Beard (1990) speculated that, in addition to sampling method biases, the highly variable population estimates derived from breeding ground surveys since the late 1970's (see Table 1) may be the result of differing sex/age class and/or feeding ground origin occupancy patterns in the breeding grounds.

During the YONAH project, nearly 3,000 individuals were photographed, and just over 2,000 were biopsied

throughout the North Atlantic in 1992 and 1993 (Smith et al., 1999). The resulting ocean-basin-wide population estimates of 10,400 (95% CI = 8,000–13,600) from biopsy data, and 10,600 (95% CI = 9,300–12,100) from photo-ID data were much larger than the estimates from the 1980's, and likely reflected a combination of population growth and reduced sampling bias (Smith et al., 1999).

Palsbøll et al. (1995) used the biopsies from the YONAH study to produce the first mark-recapture abundance estimate based on microsatellite genotyping data. Stevick et al. (2003b) later applied strict photo-ID protocols and more robust statistical analyses to the pooled mark-recapture data from YONAH and all NAHWC records collected between 1979 and 1991 to produce an abundance estimate of 11,570 (95% CI = 10,290 to 13,390) humpbacks in the North Atlantic. The Stevick et al. (2003b) method of pooling the data and applying advanced statistical analyses likely reduced the heterogeneity and small sample size biases associated with the estimates from YONAH alone (Smith et al., 1999).

An important finding of YONAH was that sex-specific abundance calculations derived from the breeding ground genetic samples produced significantly different estimates for females (1,776–4,463(95%CI)) and males (3,374–7,123 (95%CI)), and the total population estimate derived from breeding ground photo-ID and genetic tagging data alone was significantly lower than the ocean-wide estimate. However, the male-only genotype estimate was almost exactly half the winter-summer photo-ID estimate, suggesting that male-specific estimates derived from breeding grounds are more reliable than any estimate that involves sampling of females. The explanation for this is uncertain, and likely relates to sex-based differences in habitat preference, and/or migratory timing. Whatever the reason, the doubled male-only estimate agrees well with the Stevick et al. (2003b) overall photo-ID estimate of 11,570, and these two remain the most reliable estimates of North Atlantic humpback whale abundance to date.

A visual and acoustic survey of the Lesser Antilles conducted by Swartz et al. (2002) covered a broad area from Puerto Rico to Venezuela. The low detection rate from this survey (31 visual and at least 142 acoustic detections of humpbacks over the 10,900 km surveyed) reinforced earlier findings (Winn et al., 1975; Levenson and Leapley, 1978) that far fewer whales overwinter in the Lesser Antilles than in the Greater Antilles. Silva et al. (2006) conducted a short survey in 2002 in an area not covered by Swartz et al. (2003) and recorded 11 humpback whale sightings just north of Margarita Island and Los Frailes Archipelago (Venezuela). Gandilhon's (2012) line-transect surveys, which took place between January and June, 2008–11, resulted in a population estimate of 442 (95% CI = 302–442) humpbacks using the territorial waters of Guadeloupe. Peak abundance was recorded in April.

Swartz et al.'s (2002) subsequent survey from the Bahamas to the Virgin Islands in February and March of 2001 detected humpback whales throughout the entire study area south of the Bahamas, yet the 8:1 acoustic to visual detection ratio showed that visual-only surveys can greatly underestimate true whale densities in winter. Overall, the authors calculated an abundance estimate, based on sighting data, of 532 (95% CI = 260–1,088) humpback whales on the Puerto Rican-Virgin Island insular shelf.

The large-scale follow up to the YONAH project, MONAH, was conducted in January and February of 2004 and 2005, on Silver Bank only; additional sampling was also conducted on a single summer feeding ground, the Gulf of Maine. Unlike in YONAH, biopsy sampling for genotyping was the priority over photo-ID, although fluke photos were taken whenever possible. Genetic analyses from MONAH samples are currently underway, and the preliminary results will be used to generate a male-specific estimate of North Atlantic humpback abundance based upon genotyping. However, telemetry studies have shown movement throughout the greater Caribbean region within the breeding season (Kennedy et al., 2013, Fossette et al., 2014); while much of this within-season movement occurred on Silver, Navidad, and Mouchoir Banks, even small individual movements into or out of a study area could bias the capture probability assumptions used in mark-recapture analysis and affect population estimates based on such data (Hammond et al., 1990; Friday, 1997).

Population Structure

In the early 1970's, before photo-ID catalogs or genetic analysis technologies had been developed, Mitchell and Reeves (1983) and Winn and Scott (1977) proposed a distinct spatial separation of three feeding stocks on the breeding grounds with no conclusive evidence of spatial mixing. More than four decades of photo-ID analyses from the late 1970's to the present day have greatly expanded our knowledge of population structure in both the feeding and breeding grounds, and we now know that the "three-stock hypothesis" is incorrect.

Researchers aboard the *Regina Maris* opportunistically photographed humpback flukes on the breeding ground from 1977 to 1981 (Balcomb and Nichols, 1978, 1982) and were able to report the first match between a North Atlantic feeding ground (Tooker Bank, Newfoundland) and breeding ground (Silver Bank), in 1977 (Balcomb and Nichols, 1978). Extensive photo-ID analysis by Katona and Beard (1990) highlighted the presence of four, or probably five, separate feeding aggregations (Iceland/Denmark Strait, western Greenland, Newfoundland/Labrador, Gulf of St. Lawrence, and the Gulf of Maine/Scotian Shelf). Stevick et al. (2003b) later used YONAH data to define the feeding aggregation boundaries as the Gulf of Maine, eastern Canada (including Newfoundland, Labrador, and the Gulf of St. Lawrence), West Greenland, and the eastern North Atlantic (Iceland and

Norway). Genetic analysis indicated that this strong, maternally directed feeding-area fidelity had persisted over a long enough period to be evident in mitochondrial DNA structure (Palsbøll et al., 1995; see also Clapham et al., 2008) despite extensive genetic mixing on the breeding grounds.

Analysis of photos collected on Silver Bank in 1984 by Mattila et al. (1989) described 97 whales that had been previously seen in summer feeding grounds (Greenland, Newfoundland/Labrador, Gulf of St. Lawrence, Gulf of Maine) or another wintering area (Silver Bank, Puerto Rico, Virgin Bank, Anguilla Bank), as well as off Bermuda. Mattila and Clapham's (1989) photo-ID study in the northern Leeward Islands in 1985 and 1986 found nearly the same results as on Silver Bank; matches were made to all major North Atlantic feeding grounds except to Iceland and Norway in the eastern North Atlantic.

The lack of representation of eastern North Atlantic whales in these studies (Mattila et al., 1989; Mattila and Clapham, 1989) was originally attributed to the small number of catalogued whales from the eastern feeding grounds, but may also be the result of survey timing or behavioral differences between eastern and western North Atlantic whales (Stevick et al., 2016b). Martin et al. (1984) had matched whales seen off Puerto Rico and Silver Bank to the small (n=17) Icelandic catalog prior to the Mattila and Clapham studies and, as predicted, later studies documented more matches between the Antilles and the eastern North Atlantic (Clapham et al., 1993; Larsen et al., 1996; Stevick et al., 1999a, 1999b; Smith et al., 1999; Bérubé et al., 2004).

While the presence of humpbacks from all North Atlantic feeding grounds on the Antillean breeding grounds is undisputed, genetic analysis of samples collected during YONAH showed that eastern North Atlantic whales were underrepresented compared to western North Atlantic whales on Silver and Navidad Banks (Stevick et al., 2003a). Furthermore, a recent examination of photos collected between 1972 and 2014 from Antigua to Venezuela suggest that humpbacks wintering in the southeastern Caribbean are not a representative subset of those wintering off the Dominican Republic (Stevick et al., 2016b). Stevick et al. (2016b) found that animals that typically feed in the eastern North Atlantic are significantly over-represented in the southeastern Caribbean compared to animals that summer in the western North Atlantic. These findings suggest that southeastern Caribbean humpbacks represent a group of behaviorally distinct whales within the Antillean breeding grounds.

The most recent confirmation of mixing between eastern and western North Atlantic feeding stocks in the Antilles came when whales tagged on Silver Bank, Guadeloupe, and Anguilla were tracked over either full or partial migrations to both regions (Kennedy et al., 2013; Fossette et al., 2014). Interestingly, two satellite-tagged whales heading toward eastern North Atlantic feeding grounds showed ≈1,300 km of nearly identical track lines, followed by an additional ≈1,600 km of track with nearly identical heading (separated by roughly 200 km), despite the spatial and temporal separation of the tag deployments (Kennedy et al., 2013). This overlap may represent evidence for the existence of specific migratory corridors from the Antillean breeding grounds to eastern North Atlantic feeding grounds (Charif et al., 2001), and supports the findings of Horton et al. (2011) that humpbacks, like other marine animals (Gaspar et al., 2006; Trathan et al., 2008), can navigate across long distances with remarkable precision.

In addition to apparently unequal breeding ground occupancy rates by whales from different feeding grounds (Stevick et al., 2016b), Stevick et al. (2003a) found that different sex and age classes arrive on the breeding grounds at different times; males were observed as much as three weeks earlier than females (with or without calves) on Silver and Navidad Banks. This is consistent with studies based upon whaling catches made in Australia and New Zealand, which also show a migration that is staggered by sex, age class, or female reproductive condition (Chittleborough, 1965; Dawbin, 1966, 1997).

Genetic analyses indicate the existence of a second, and perhaps even third, as-yet undiscovered North Atlantic breeding ground (Palsbøll et al., 1995; Larsen et al., 1996). However, speculation that the Cape Verde Islands (CVI) may represent one of these unknown breeding grounds seems unlikely (Larsen et al., 1996) due to the relatively small local humpback population size. Additionally, Winn et al. (1981) compared songs between the West Indies and the CVI and found no difference; this might suggest no stock separation, but song is known to be at best a crude and sometimes unreliable indicator of stock division (Garland et al., 2012).

More recently, Jann et al. (2003) documented a photo-ID match between a whale seen in the CVI and the Denmark Strait (off Iceland), yet the low photographic sample size in both regions cannot conclusively support the hypothesis that the CVI is the primary migratory destination for eastern North Atlantic humpbacks. While a surprising recent discovery of 4 humpback whales photographically identified in both Guadeloupe and Boa Vista (CVI) (Stevick et al., 2016a) further underscores the suggestion that there are behaviorally distinct groups within the overall North Atlantic population, it cannot fully explain the undiscovered breeding ground.

Telemetry results highlight the vastly different distances over which individuals from different feeding grounds must migrate to reach the breeding grounds. For humpback whales that feed off Norway, this distance is approximately three times that of Gulf of Maine whales, and tag data have documented correspondingly large differences in transit times (Kennedy et al., 2013). The cost of this extended migration vs. the overall benefit to an individual humpback are difficult to define or measure, yet the energetic

requirements for a full migration between the Antilles or the CVI and the eastern North Atlantic may be high enough to deter yearly full migrations. This disparity in migratory distance and the resultant decisions made by individuals regarding migratory timing and extent may partially explain the spatial and temporal segregation of humpbacks that feed in the eastern vs. western North Atlantic on the breeding ground.

Habitat Use and Within-season Movement

Winn et al. (1975) noted that, during the breeding season, humpbacks were found "almost exclusively" on banks between 10 and 100 fathoms (18–180 m) deep, yet there was little or no sighting effort in the deep waters off the shelf break. Roden and Mullen (2000) recorded 12 humpback sightings in an average depth of 2,877 m during their cetacean abundance survey between Guadeloupe and western Cuba. Mignucci-Giannoni (1998) compared humpback sightings (published and unpublished, up to 1985) off Puerto Rico and the Virgin Islands and found that those whales also prefer shallow, nearshore waters with little slope. A recent study off the western coast of Puerto Rico found that mother-calf pairs were most often found nearshore in shallow water, while singers were found more frequently along the shelf edge than other areas in Mona Passage (MacKay et al., 2016). Depth did not appear to be a factor for the presence of single non-singing whales (MacKay et al., 2016).

From earlier studies, it was estimated that approximately 85% of the whales on the breeding ground were found on Silver and/or Navidad Banks each year, and Silver Bank appeared to have the highest calf density in the West Indies (Winn et al., 1975; Balcomb and Nichols, 1982). Virgin and Anguilla Banks, Mona Passage (Puerto Rico), and Samaná Bay (DR) also host mothers and calves, though in much smaller numbers. There was a virtual absence of calf sightings on Navidad Bank (with very little reef protection) between 1977 and 1981, which led Whitehead and Moore (1982) to speculate that mother-calf pairs prefer the calm waters alee of reefs or large coral heads like those on Silver Bank. However, calves were observed there during YONAH surveys (Robbins et al., 2001; Mattila et al.[2]), so the relative suitability of this habitat for mothers is unclear.

The preference for Silver and Navidad Banks over other banks with very similar oceanographic characteristics has been a matter of some discussion. The waters around Los Frailes Archipelago and Margarita Island, Venezuela, for example, appear to have represented populous humpback wintering grounds in the late 1800's (Townsend, 1935; Reeves et al., 2001). While they possess similar topographic and bathymetric features as Silver and Virgin Banks, very few humpbacks have been seen there since the 1970's (Winn et al., 1975; Swartz et al., 2003; Silva et al., 2006). Whitehead and Moore (1982) proposed that the appeal of Silver and Navidad Banks is the presence of many whales. In other words, Silver and Navidad Banks seem integral to the humpback whales' mating system in that the males are more likely to congregate and compete in areas which have value to the highest number of females.

Individual movements among different areas of the breeding range had been shown through a small number of photo-ID matches of whales seen off Puerto Rico, Anguilla, Virgin Bank, and Silver Bank at different times in the same winter (Mattila et al., 1989). Overall, the observed direction of movement was east to west along the Antillean Chain. Unfortunately, mark-recapture studies do not permit finer-scale habitat-use descriptions.

Telemetry studies have shown that individuals travel to areas relatively distant from densely populated banks, including to waters off the Turks and Caicos Islands, the northern coast of Haiti, Antigua, Barbuda, Anguilla, and the Virgin Islands (Kennedy et al., 2013; Fossette et al., 2014). These studies also show that whales tagged in the West Indies breeding grounds also travel relatively long distances throughout the island chain within a breeding season.

Reproductive Behavior

Winn et al. (1971) recorded humpbacks producing highly patterned sounds in an ordered sequence during a brief, exploratory acoustic survey in the winter of 1969 in Mona Passage, Puerto Rico; these results were consistent with studies from Bermuda, which resulted in the first formal description of humpback whale song around this same time (Payne and McVay, 1971). While genetic analysis technology was still in its infancy, Winn et al. (1973) managed to collect and analyze a skin sample from a singing whale and found that it lacked the sex chromatin body normally found in the nuclei of mammalian female skin. This fact, coupled with whaling records stating that the lone individuals (often found outside of calving bays) were always males (Nordhoff, 1856), led Winn et al. (1973) to hypothesize that singing whales are generally young, lone males; this suggested that the primary function of singing was related to the mating system. Whitehead and Moore (1982) found that the highest singer density occurred consistently over flat bottom areas of Silver, Navidad, and Mouchoir Banks. That singers are male has been confirmed by numerous subsequent studies worldwide (Glockner-Ferrari and Ferrari, 1981; Glockner, 1983).

Winn and Winn (1978) conducted a detailed analysis of all acoustic recordings collected from 1969 through 1977 from Grand Turk Island (Bahamas) to Venezuela. Results from this analysis included a detailed description of the humpback whales' acoustic repertoire in the Antilles, a description of yearly changes in the song, and a suggestion

[2]Mattila, D. K., M. Bérubé, R. Bowman, C. Carlson, P. J. Clapham, A. A. Mignucci-Giannoni, P. Palsbøll, J. Robbins, P. Stevick, and O. Vasquez. 2001. Humpback whale habitat use on the West Indies breeding grounds. Sci. Committee Doc. SC/53/NAH3 (unpubl.), Int. Whal. Comm., Camb. Engl. (avail. from IWC, Camb., U.K.).

of local acoustic "dialects" within the breeding range. The authors hypothesized that the function of the song is to locate breeding areas, establish territory, maintain contact with groups, and/or identify individuals. Today, song is widely believed to represent an advertisement by males to attract females (Clapham, 1996), and also possibly to mediate male intrasexual interactions (Darling and Bérubé, 2001).

Assemblages of humpback whales featuring highly aggressive behavior, often termed "competitive groups" (Clapham et al., 1993) or "rowdy groups" (Tyack and Whitehead, 1983), had been observed with frequency in the West Indies and elsewhere. This behavior was seen as intra-sexual competition among males for access to a female. A study in Samaná Bay between 1989 and 1991 used molecular sexing and photo-ID to confirm this assumption (Clapham et al., 1993). Analysis of the group composition confirmed the hypothesis from earlier work that most competitive groups, although unstable, usually contain a female (nuclear animal, NA), a male principal escort (PE), and various other secondary escorts and challengers. The authors noted that the fact that relatively few principal escort displacements have ever been observed could mean that the PE had already mated with the NA and was mate-guarding (thus making her less attractive to the other males in the group).

Prior to the Clapham et al. (1993) study, competitive groups were often thought to consist exclusively of multiple mature males competing for a mature female. However, the molecular sexing technique allowed the authors to further assess the composition and role of these groups within the breeding system. Several all-male competitive groups were discovered; such assemblages may serve as an opportunity for dominance sorting between individuals who are likely to encounter each other with some frequency on the breeding grounds.

The presence of apparently mutually non-agonistic male pairs within competitive groups may indicate cooperation between males to secure a female, but it is not clear how this cooperative behavior would increase the reproductive success of non-mating, non-kin individuals. Female aggression against a sub-adult male was noted and suggests active selection, rather than passive acceptance, of a PE in some cases (Clapham et al., 1993). Additionally, photo-ID uncovered the presence of some competitive groups containing more than one female or a sub-adult male, urging caution in future research when making sex and age assumptions about such groups (Clapham et al., 1993).

Conservation

The first conservation efforts aimed at protecting humpback whales in the West Indies occurred in the DR. The critical importance of Silver and Navidad Banks to humpback whales and other cetaceans was reflected in the designation of the Silver Bank Marine Mammal Sanctuary in October of 1986. This was effectively the world's first national humpback whale sanctuary and, as such, the designation represented a major global conservation milestone for the species. The sanctuary (now named the Silver and Navidad Banks Sanctuary) was expanded on 5 July 1996 to include Mouchoir Bank, Navidad Bank, Samaná Bay, and the waters in between.

In October of 2010, the French government established a marine sanctuary, named Agoa, which covers the territorial waters of St. Martin, St. Barthelemy, Guadeloupe, and Martinique in the Lesser Antilles. This new sanctuary is governed under the Specially Protected Areas and Wildlife (SPAW) protocol, established under the Cartagena Convention. The Silver and Navidad Banks and Agoa sanctuaries, together with protected waters off Bermuda and Stellwagen Bank (off Massachusetts), are part of a larger "sister sanctuary" program designed to improve humpback conservation by encouraging management collaboration between nations that host breeding, feeding, and/or migrating humpback whales.

Since commercial whaling in the North Atlantic ceased in the mid-1950's, there have been relatively few threats to humpback whales in their primary North Atlantic breeding range. Elsewhere in the North Atlantic (particularly on the feeding grounds), the major anthropogenic threats are entanglement in fishing gear and ship strikes (Laist et al., 2001; Robbins and Mattila, 2004; Johnson et al., 2005).

In the breeding range itself, disturbance from nature-focused tourism and oil and gas exploration (notably off Venezuela) are the principal conservation concerns. Whale-watching in the Antilles began in the 1980's on Silver Bank and in Samaná Bay and by the mid-1990's had spread to the Turks and Caicos, Puerto Rico, and several locations in the Lesser Antilles (Hoyt and Hvenegaard, 2002). The DR government has passed regulations requiring permits for access to the Silver and Navidad Banks Sanctuary in an attempt to limit the human disturbance to the whales in their territorial waters, but unregulated whale-watching throughout the breeding range is almost inevitable and likely to increase over time. Additionally, the growing oil and gas industry off the coast of Venezuela increases the potential for anthropogenic disturbance and/or mortality of humpbacks overwintering there.

An example of directed conservation efforts in the DR occurred in 2005, when a group called Los Amigos de los Delfines conducted a cetacean survey of the waters off the southeastern corner of Hispaniola. Whaley et al. (2008) observed a group of 4 humpbacks (including a calf) just off Saona Island; these were the first confirmed sightings of humpbacks off the southern coast of the DR since the early 1980's (Whaley et al., 2008). The authors' efforts in detailing the harassment of these animals prompted the Dominican government to facilitate the creation of a training program and associated "Guide to Good Practices for the Conservation of Marine Mammals."

The need for effective conservation efforts was underscored by a recent

passive acoustics study (2008), conducted by the NMFS National Marine Mammal Laboratory and the Bioacoustics Research Program at Cornell University, which found that humpback whales in Samaná Bay altered their song production in the presence of vessel noise (Berchok et al.[3]) While adherence is not yet mandatory, the government strongly encourages all mariners within the DR to adopt the actions outlined in the guide.

Understanding the fine-scale spatial and temporal distribution and behavior of animals within regions of high exposure to anthropogenic threats is essential for conservation and management of humpbacks world-wide. Satellite telemetry has shown that tagged humpbacks spent less than half of the tag duration within marine sanctuary boundaries (Kennedy et al., 2013), proving that efforts aimed at the conservation and management of this species need to occur on an ocean-basin-wide level in order to protect these highly mobile animals. A management plan for the Silver and Navidad Banks Sanctuary was recently finalized and represents a major step forward in the protection of all species which depend upon the waters of the DR, yet effective multi-national collaboration is still lacking range-wide.

Conclusions

The evolution of humpback whale research methods and knowledge in Antillean waters is largely representative of studies of this species elsewhere in the world (i.e. Darling and McSweeney, 1985; Baker et al., 1994; Helweg et al., 1998; Stevick et al., 2004; Robbins and Mattila, 2006; Barlow et al., 2011, and many others). Much has been learned about humpbacks in the wider Caribbean region since research began there more than half a century ago. Today, we have a reasonably good picture of the occurrence and distribution of the species in much of the West Indies, which clearly represents the principal mating and calving ground for North Atlantic humpback whales.

Knowledge Gaps

Smith and Pike (2009) outline the seven major unknown factors, or enigmas, of North Atlantic humpback whale population dynamics and biology. While many of these enigmas pertain to feeding season population dynamics, large gaps in knowledge of the breeding ground population structure, temporal distribution, and population abundance still exist, despite decades of research throughout the region.

The apparent failure of humpbacks to repopulate the Windward Islands region to levels suggested by historical whaling catches is difficult to understand, given the general resilience of this species elsewhere in the world, and has yet to be explained. Genetic analysis, a recent reexamination of over 40 years of fluke photographs showing unequal representation of animals from different feeding grounds on the breeding ground, and differences between population abundances estimated on the feeding ground vs. the breeding ground suggest two things: that there is a 3rd as-yet-undiscovered breeding ground in the North Atlantic (Palsbøll et al., 1995; Larsen et al., 1996; Smith and Pike, 2009; Stevick et al., 2016b), and that there are likely behaviorally distinct groups of humpbacks on the breeding grounds as well as the feeding grounds (Stevick et al., 2003a; Stevick et al., 2016b). Humpbacks have been known to overwinter and engage in breeding behavior (notably singing and competitive group activity) on the feeding grounds and during migration (Swingle et al., 1993; Robbins et al., 2001; Barco et al., 2002; Clark and Clapham, 2004) yet whether breeding outside of well-described areas occurs on a large enough scale to influence the population's genetic profile and abundance estimates is unknown. While the recent discovery of multiple instances of exchange between Guadeloupe and the CVI (Stevick et al., 2016b) is an important piece of the puzzle, it seems unlikely that this exchange could fully account for the feeding vs. breeding ground population estimates or the undiscovered breeding ground.

Knowledge gaps regarding breeding ground population dynamics exist, in part, due to the bias resulting from inadequate spatial and temporal survey coverage in the West Indies. In order to increase genetic, photographic, and/or acoustic sample sizes, the vast majority of projects conducted in the area were designed to coincide with the highest densities of animals (e.g., January through March within the Silver, Navidad, and Mouchoir Banks complex). Unfortunately, this strategy likely excludes members of behaviorally distinct groups from being sampled, thus biasing the resulting conclusions about North Atlantic humpback populations overall. Additional telemetry, photo-ID, and biopsy studies that cover a greater spatial and temporal scale are clearly needed in order to fully understand North Atlantic humpback whale population dynamics. Continued and expanded multi-national research collaboration is essential to the success of such projects and should be considered the highest priority for creating and executing an effective management plan.

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Asphyxiation of an Endangered Cook Inlet Beluga Whale, *Delphinapterus leucas*

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ABSTRACT—The isolated population of Cook Inlet beluga whales, Delphinapterus leucas*, is endangered under the U.S. Endangered Species Act (ESA). They reside year-round in the Cook Inlet tidal estuary in southcentral Alaska, near Anchorage. Due to their ESA status, information on causes of mortality are important. A dead beluga was reported in Turnagain Arm, Cook Inlet, on 7 Oct. 2013, and a necropsy was performed two days later. The beluga was a robust, apparently healthy adult male ~40 years old. Cause of death was determined to be asphyxiation caused by a starry flounder,* Platichthys stellatus*, found lodged in the pharynx at the goose beak, dislocating the larynx. Prey anatomy such as spines, body shape, and backbone rigidity may increase the risk of choking in beluga whales and other cetaceans. This is the first known death by asphyxiation of the 49 Cook Inlet beluga deaths investigated in the last 18 years, indicating that it is rare and not likely to be a significant cause of mortality. It is important, however, to monitor and document all sources of mortality given the status of this endangered population.*

Introduction

The Cook Inlet beluga whale, *Delphinapterus leucas,* is nonmigratory, residing year-round in a semi-enclosed tidal estuary in southcentral Alaska. The population is genetically and spatially isolated from all other beluga populations (O'Corry-Crowe et al., 1997; Laidre et al., 2000). Once an important subsistence species for Alaska Natives, unregulated hunting led to a substantial decline in the Cook Inlet beluga population between 1994 and 1998 (Hobbs et al., 2000). The population has continued to decline despite a hunting moratorium and co-management agreements between the National Marine Fisheries Service (NMFS) and Alaska Native organizations that limited the hunt (Hobbs et al., 2000, 2015). In 2016, the population was estimated to be 328 whales (Shelden et al.[1]). The status of this population, with no known cause for a continued decline, elevates the need to necropsy all dead belugas for causes of mortality. NMFS developed a stranding response plan[2] for Cook Inlet belugas in 2009, authorizing necropsies of dead Cook Inlet belugas.

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Methods

Study Area

Cook Inlet (Fig. 1) is a 180 mi long, 39,325 mi^2 mass of water bordering the Gulf of Alaska and adjacent to the city of Anchorage in south central Alaska. It is characterized by shallow, soft, mixed benthic sediment, mud flats, large tidal fluctuations (30+ ft), and active seismic and volcanic contributions. Approximately 347,000 people (about half of the population of the State of Alaska) reside adjacent to Cook Inlet. Most cities and villages are located on the east side, which is accessible by both road and rail line. The west side of the inlet is sparsely populated and is only accessible by air or boat.

On 7 Oct. 2013, a beluga whale was reported stranded in Turnagain Arm (Fig. 1). Weather prohibited examination until 9 Oct. 2013, when the carcass was accessed by helicopter and approached on foot. The carcass had moved west of the original stranding location, presumably having floated and re-stranded on the outgoing tide.

Examination and Sample Collection

The examination included external, subcutaneous, respiratory, digestive, lymphoid, urogenital, reproductive, and endocrine systems. Representative tissues from all body systems were collected fresh (and later frozen at -20°C) and also fixed in formalin for histological examination. Bacteriology tests were performed on blowhole and fecal swabs (Athens Vet Diagnostic Lab[3]) and virological tests were conducted for agents such as herpes virus, influenza, and mobillivirus. Teeth were aged by D. Vos[4] and stomach contents were analyzed by the Alaska Department of Fish and Game, Arctic

[1]Shelden, K. E. W., R. C. Hobbs, C. L. Sims, L. Vate Brattström, J. A. Mocklin, C. Boyd, and B. A. Mahoney. 2017. Aerial surveys, abundance, and distribution of beluga whales (*Delphinapterus leucas*) in Cook Inlet, Alaska, June 2016. AFSC Processed Rep. 2017-09, 62 p. Available at http://www.afsc.noaa.gov/Publications/ProcRpt/PR2017-09.pdf.

[2]Stranding Response Plan avail. at https://alaskafisheries.noaa.gov/sites/default/files/beluga_stranding_plan2009.pdf, accessed 25 Apr. 2016.

[3]Mention of trade names or commercial firms does not imply endorsement by the National Marine Fisheries Service, NOAA.

[4]Teeth were aged by Daniel Vos, Anchorage, AK. Growth layer groups are laid down annually in Cook Inlet belugas.

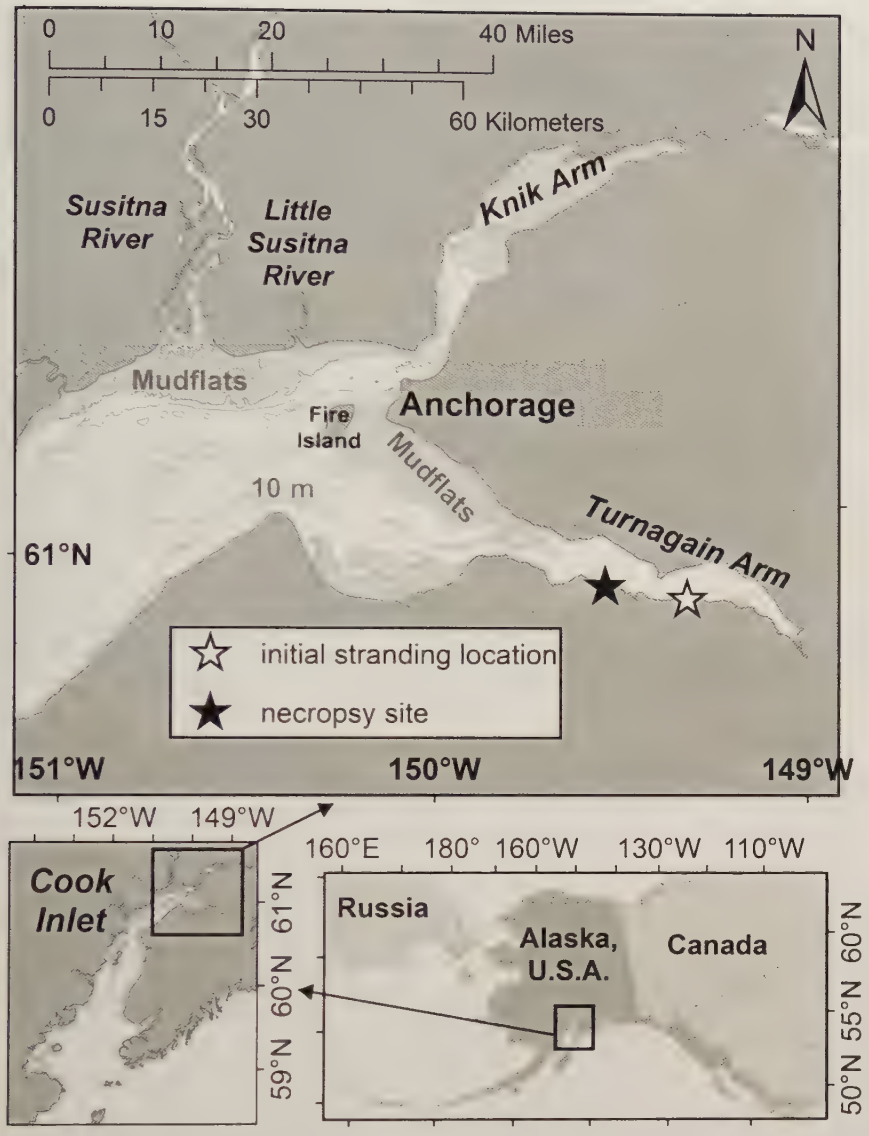

Figure 1.—Initial stranding location and necropsy site for a male beluga whale that died of asphyxiation in Cook Inlet, Alaska, in October 2013.

Marine Mammal Program, Fairbanks, Alaska.

Results

Gross Findings

External examination revealed an adult male in good body condition determined by distinct and well-developed "rails" (thick folds of blubber along the ventral surface) as well as internally abundant blubber stores and fat at the base of the heart. The abdomen was markedly bloated and blood was draining from the eye, anus, and preputial opening. The carcass was mildly decomposed and largely intact with minimal scavenging by birds (Fig. 2). This whale was well known, having been identified in photographs every year from 2004 to 2014 (McGuire[5]).

A large flatfish was found firmly lodged in the pharynx, near the constriction named the "goose beak." This fish was folded with the head and tail projecting outward and lateral spines down through the esophagus. It could not be easily removed from the mouth outward. It appeared that the fish had displaced the goose beak from the nasopharynx (Fig. 3). Dark red fluid was draining from the blowhole. The tracheal and bronchial mucosa were deeply discolored (from red to black), and covered in granular black to tan material (most likely aspirated food material). Blubber near the ventral midline of the cervical region was markedly discolored, red, and mottled. On cross section, some of these areas had red discoloration radiating outward from the muscle layer. This trauma appeared to be the result of fish spines in the esophagus.

Cause of death was determined to be asphyxiation due to displacement of the goose beak by a starry flounder, *Platichthys stellatus* (Fig. 4). The flounder appears to have been too large to fit into the pharynx as it was folded to the side of the goose beak and embedded into the esophagus. It could be neither regurgitated nor swallowed because of the direction of the spines and its size and orientation. Further evidence of choking included a large amount of aspirated material, likely digesta, in the lungs.

Other findings, not related to the cause of death, included irregular lymph nodes (the prescapular was irregular and multinodular, and caudal mediastinal and hilar lymph nodes were greatly enlarged and mottled). The liver had autolyzed and the spleen was congested and enlarged. Thyroid and pituitary glands were not examined. The urinary bladder was not observed. The intestines were discolored dark red and there was little content in the sections examined. Multiple, small mineralized nodules (0.5–2 cm in diameter) were present in both kidneys (17 in the left, 36 in the right) which contained nematodes, *Crassicauda giliakiana*. No parasites were observed in the lungs. There were no other significant gross findings.

The stomach was collected intact and contained a Pacific cod, *Dadus microcephalus*, otolith; Arctic lamprey,

[5]McGuire, Tamara. LGL Research Associates, Anchorage, AK, Personal commun., 2016.

Lampetra camtschatica, mouth parts; fragments of invertebrates from polychaetes (Polynoidae) and *Nereis* sp.; and shrimp (Crangonidae); and a few nematodes.

Histopathologic and Ancillary Findings

Laboratory results of blowhole swabs were negative for influenza virus, but positive for beluga herpesvirus. Beluga herpesvirus is endemic in Cook Inlet beluga whales (Burek-Huntington et al., 2015; Davison et al., 2017) and does not cause symptoms in healthy animals and no symptoms (e.g., skin lesions) were observed. There was some intermyofiber fibrosis in the heart, particularly the left ventricle. This has been seen quite frequently in older belugas and appears to be a change that comes about as the animal ages. Subsequent aging of the teeth determined that this whale was a 40 yr old adult (Vos[4]). The prescapular lymph node was in good histologic condition and did show a pyogranu-

Figure 2.—Ventral and dorsal surfaces of the male beluga whale (2013-CIB-04) prior to start of the necropsy.

Figure 3.—Internal damage caused by displacement of the goose beak during ingestion of a flounder by a male beluga whale (2013-CIB-04). Solid arrows (on right) indicated the ventral hemorrhage in the esophagus. Open arrows (at left) indicate the goose beak and position of the flounder.

Figure 4.—Top: starry flounder, *Platichthys stellatus*, ingested by the male beluga whale (2013-CIB-04). Bottom: comparison image of an intact starry flounder (source: https://alaskafisheries.noaa.gov/habitat/nearshore-fish-photos, and https://alaskafisheries.noaa.gov/mapping/oreZoneMvcServicesBeta/FishAtlas/FishDisplayPage?spCode=FLOUNST accessed 1 Apr. 2017).

lomatous lymphadenitis of unknown cause. It was most likely related to drainage from subcutaneous parasites or from the chronic lesion seen in the neck.

There was extensive inflammation associated with the submucosal glands in the esophagus and some chronic fibrosis in skeletal muscle in the area at the site of the obstruction, which was chronic and active. It is possible that this chronic fibrosis and abnormalities in the skeletal muscles of the throat may have predisposed the animal to asphyxiation. There was some minor, chronic inflammation in the lungs, and no direct evidence of parasites was observed; however, there were frequent, occasionally mineralized, Splendore-hoeppli bodies lining the bronchi and bronchioles. This feature is often associated with lung worms in belugas (Burek-Huntington et al., 2015). A few bronchi in the lungs contained a large amount of debris, including some skeletal muscle (possibly fish), corroborating that some food had been aspirated into the lungs. Overall, there was nothing within the histopathologic findings to indicate another cause of death other than asphyxiation.

Discussion

In cetaceans, the anatomy of the esophagus and the trachea are completely separate and no air is inhaled through the mouth. The esophagus is bifurcated by a cartilaginous extension of the trachea called the goose beak (Fig. 5). This cartilaginous organ bridges the gap between the nasal passages and the trachea, and while it is not attached, it is tightly fitted within the animal, and designed to keep anything but air out of the lungs. The goose beak can be dislocated if the animal swallows something too large to pass through the bifurcation.

Asphyxiation due to laryngeal displacement has been documented in cetaceans, most often in bottlenose dolphins, *Tursiops truncatus* (Harmer, 1927; Johnston and Ridgway, 1969; Berrow and Rogan, 1997; Bossart et al., 2003; Watson and Gee, 2005; Mazzoil et al., 2008; Mignucci-Giannoni et al., 2009; Stolen et al., 2013; Barros and Odell[6]) and *T. aduncus* (Byard et al., 2003, 2010; Kemper et al., 2005). Choking on prey has also been reported for other wild cetacean species such as long-finned pilot whales, *Globicephala melas* ((IJsseldijk et al., 2015); harbor porpoise, *Phocoena phocoena* (Orr, 1937; Scheffer and Slipp, 1948; Scheffer, 1953; Hult et al., 1980); Pacific white-sided dolphins, *Lagenorhynchus obliquidens* (Houck, 1961); short-beaked common dolphin, *Delphinus delphis* (Krivokhizhin and Birkun, 1991); Atlantic spotted dolphin, *Stenella frontalis* (Mignucci-Giannoni, 1996); whitebeak dolphin, *L. albirostris* (Scottish Agri-

[6]Barros, N. B., and D. K. Odell. 1995. Prey-induced mortality in coastal bottlenose dolphins from the southeastern United States. *In* Abstracts of XX reunión internacional para el estudio de los mamíferos marinos. La Paz, Baja Calif. Sur, Méx., p. 54.

cultural College[7]); and minke whale, *Balaenoptera acutorostrata* (Knowles, 2000).

Cook Inlet beluga hunters recall a time "a beluga was found thrashing around in shallow water with a flounder stuck in its throat" (Huntington, 2000). We know of only one other circumstance of asphyxiation in a wild beluga, an animal that attempted to ingest a 20 lb. (9.1 kg) cod (Fay, 1971). Fay (1971) noted that fish larger than 9 lb. (4.1 kg) were rarely consumed. Salmon were the largest fish found in beluga stomachs examined by Quakenbush et al. (2015), and none were larger than 7.7 lb (3.5 kg). Asphyxiation has occurred in captive belugas (Hult et al., 1980; Casey, 2015) and Pacific white-sided dolphins (Ridgway and Johnston, 1965), and is a known concern for captive beluga whales that may also ingest toys or other foreign objects (Woodie[8]).

Watson et al. (2015) theorized that death due to asphyxiation is caused by ingestion of extra-large or unusual prey such as small sharks (Harmer, 1927; Orr, 1937). Barros and Odell[6] suggest ingesting prey with "dangerous" appendages such as dorsal or pectoral spines could be a risk factor. Although this starry flounder falls into the typical length of prey (17–64 cm) consumed by Cook Inlet belugas (Quakenbush et al., 2015) it is an unusually shaped prey item in that it is a wide flatfish with prominent spines on two edges (Fig. 4). In addition to spines, flatfish may have a harder backbone due to their unique anatomy, making them less flexible when swallowed (IJsseldijk et al., 2015). IJsseldijk et al. (2015) documented fatal asphyxiations in two long-finned pilot whales caused by another flatfish, the common sole, *Solea solea*.

Due to this beluga's excellent body condition, and both chronic and acute wounds in the larynx, consuming flatfish may have been a repeated behavior for this particular animal that ended fatally in this instance. Starry flounder, as well as other flatfish species, are known prey items for Cook Inlet and western arctic beluga whales (Fay, 1971; Quakenbush et al., 2015) and may have been the preferred prey of this individual whale during the fall (when it died) following the end of anadromous fish runs in the inlet. While we do not consider asphyxiation during feeding to be related to the decline of the Cook Inlet beluga population, it is nonetheless noteworthy and demonstrates the need to document causes of death through necropsies, when possible, for these critically endangered whales.

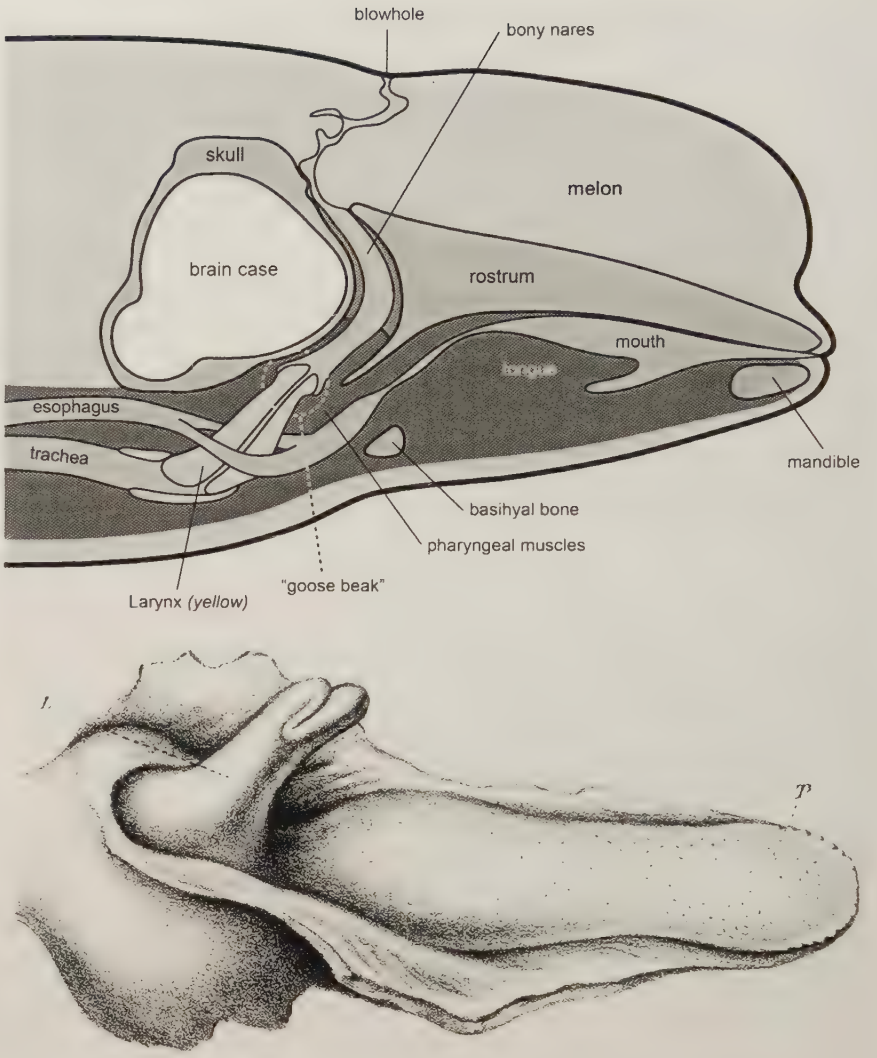

Figure 5.—Schematic of the respiratory and gastrointestinal tract of a beluga showing the location of the goose beak (illustration by Uko Gorter) above, and scientific illustration, below, showing the tongue (T) and larynx (L) from Watson and Young (1880).

Acknowledgments

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[7]Scottish Agricultural College. 2000. Cetacean strandings investigation Scotland Project report to the then Dep. Environ., Transport Regions, CR0179, Inverness, Scotl., 67 p. (cited in Mignucci-Giannoni et al. (2009)).

[8]Woodie, Derek. Marine mammal trainer, Alaska SeaLife Center, Seward, AK, Personal commun., 2015.

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Preferred paper length ranges from 4 to 12 printed pages (about 10-40 manuscript pages), although shorter and longer papers are sometimes accepted. Papers are normally printed within 4-6 months of acceptance. Publication is hastened when manuscripts conform to the following recommended guidelines.

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Submission of a manuscript to the *Marine Fisheries Review* implies that the manuscript is the author's own work, has not been submitted for publication elsewhere, and is ready for publication as submitted. Commerce Department personnel should submit papers under a completed NOAA Form 25-700 (available from the SPO website).

Manuscripts must be double-spaced throughout, and a complete manuscript normally includes a title page, a short abstract, text, literature citations, tables, figure legends, footnotes, and the figures. The title page should carry the title and the name, department, institution or other affiliation, and complete address (plus current address if different) of the author(s). An "Acknowledgments" section, if needed, may be placed at the end of the text. Use of appendices is discouraged.

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Keep titles, headings, subheadings, and the abstract short and clear. Because abstracts are circulated by abstracting agencies, it is important that they represent the research clearly and concisely. Headings within each section must be short, reflect a logical sequence, and follow the rules of multiple subdivision (i.e., there can be no subdivision without at least two items).

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The entire text should be intelligible to interdisciplinary readers; therefore, all acronyms, abbreviations, and technical terms should be spelled out the first time they are mentioned. The scientific names of species must be written out the first time they are mentioned; subsequent mention of scientific names may be abbreviated. Follow the U.S. Government Printing Office Style Manual (2008 ed.) and the Scientific Style and Format: the CSE Manual for Authors, Editors, and Publishers (2014, 8th ed.) published by the Council of Science Editors.for editorial style, and the most current issue of the American Fisheries Society's Common and Scientific Names of Fishes from the United States and Canada for fish nomenclature. Only journal titles, scientific names (genera and species), and vessel names should be italicized. Dates should be written as follows: 11 November 2013. Measurements should be expressed in metric units, e.g., metric tons as (t); other equivalent units may also be listed in parenthesis. Common abbreviations and symbols such as mm, m, g. ml, mg, and °C (without periods) may be used with numerals. The numeral one (1) should be typed as a one, not as a lower-case el (l). Write out the numbers zero through nine unless they form part of measurement units (e.g., nine fish but 9 mm).

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